

ABSTRACT

Title of Document: INFLUENCE OF MAP RESOLUTION ON
SEASCAPE ECOLOGY OF REEF FISH

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Characteristics of benthic maps are controlled by the spatial and thematic resolutions used in map production. The implications of these production decisions on the inferences that can be drawn from the maps are poorly understood. I addressed this need by quantifying the differences among common map types, considering how map type affects inferences of fish and benthic communities at the patch level, and then evaluating the influence of map type on ecological neighborhood analysis of reef fish. Results indicated that hard bottom types, especially patch reefs and colonized pavement, were among the most sensitive to changes in spatial resolution of maps. In contrast, linear reef and continuous seagrass features were characterized quite consistently regardless of spatial resolution. Multivariate analyses indicated that both the fish assemblages and benthic characteristics of reef types overlapped considerably. In contrast, shelf position (inside versus outside of lagoons) showed clear differences in both environmental variables and fish assemblage composition. In general, the results of multivariate analyses suggest that knowledge of the overall fish

assemblage or fine-scale environmental characteristics could not be used to predict reef type or vice versa. Furthermore, spatial scale of benthic maps did not affect results when analyses were conducted at the patch level. In addition, a multi-scale landscape analysis was conducted wherein correlations between fish assemblages and surrounding landscape variables were measured using univariate linear regression for a range of scales between 25 and 800 m. The strength of the associations as a function of scale exhibited one of 6 response curve forms and was used to identify the scale that best correlates fish with their surrounding habitat. In these analyses, individual landscape variables explained a maximum of only 25% of the variability in fish distributions. Use of different input maps in many of these analyses resulted in a changed perception of either the strength of peak correlation at a given scale, or the scale at which peak correlations occurred. Overall, the findings revealed which aspects of coral reef ecosystems are sensitive to map scale and advise scientists and managers on map production and use in similar settings.

INFLUENCE OF MAP RESOLUTION ON SEASCAPE ECOLOGY OF REEF
FISH

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Dedication

For my family

Acknowledgements

Intellectual property can be a fuzzy business when you interact with creative, smart, diverse people every day. While the following dissertation is my own, working and playing with everyone in NOAA's Biogeography Branch for the last ten years has shaped me in both person and profession. I am grateful for each one of them. The conversations, debates, disagreements, successes, and companionship that we have shared are dear to me. I hope I can give to them as much as they have to me.

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Chapter 1: Dissertation Introduction

Statement of the Problem

Reef fish assemblages are shaped by processes operating at a range of spatial scales. Rugosity of a small section of a reef, the general type of the overall reef patch, and even the mosaic of habitats around those reef types can play roles in shaping fish assemblage structure. Most often, researchers seek to identify the determinants of assemblage structure at the finest scales (sub-meter) by examining habitat characteristics within the immediate environment of the community of interest. Gaining in number, including the present dissertation, are studies conducted at the reef patch and landscape scale (10-100's of meters). To understand the broader-scale influences of reef type and landscape patterns on fish assemblages, scientists must rely on their best window into the fish's landscape: benthic maps produced through remote sensing. The unifying theme of each chapter in this dissertation is understanding how characteristics of those maps can shape the perception of associations between fish and their habitats.

Do reef types depicted in benthic maps represent specific fish assemblages?

Benthic maps have emerged as a key tool in ecological studies of coral reefs. Benthic maps, however, are broad-scale characterizations that lack the detailed environmental attributes that have been the focus of most prior studies of reef fish habitat (Diaz et al. 2004). Instead, maps of reef ecosystems are often produced with more general attributes that reflect benthic features depicted at broader scales

(Sheppard et al. 1995, Mumby et al. 1997, Chauvaud et al. 1998, Franklin et al. 2003, Hochberg and Atkinson 2003, Lundblad et al. 2006). In benthic maps produced for management, reef types are typically delineated in rather general categories simply as “coral” or “reef” or sometimes more specifically as rubble, pavement, patch reef, and other generalized classes (e.g. FMRI 1998, Kendall et al. 2001, Franklin et al. 2003, NOAA NCCOS 2005, Battista et al. 2007a, b). In addition, general map categories are depicted at spatial scales that are much coarser than the sub-meter scales of most studies linking fish to benthic habitat. This results in a disconnect between the intensively studied fish/habitat relationships measured at fine scales and the broad scales of habitat classification and feature delineation in benthic maps (Diaz et al. 2004).

Recently, reef ecologists have attempted to bridge the gap between their understanding of fish distributions based on finer-scale measures of environmental variables and these broader landscape classifications or reef zones. The key question for research and management of how well typical map classifications represent local substrate composition or fish assemblages remains largely unanswered.

Does the landscape around a fish assemblage influence its composition?

The previous section dealt with predicting fish assemblages on specific patches of mapped reef types. Considered here are the influences that the surrounding habitats may have on fish assemblages. Studies of fish assemblages within single habitat types without reference to the influence of the adjacent seascape elements often do not completely explain patterns in assemblage structure. This is because the fish assemblage at a given site will not only be influenced by the habitat at that site,

but also by direct or indirect interaction with other habitats occurring some distance away. Organisms may undergo direct migrations across several habitat types to fulfill some aspect of their ecology or life history such as foraging or spawning. Interactions across two or more habitat types occur at a range of spatial scales depending on the mobility and life history requirements of the organisms involved and the composition of nearby landscape elements. For example, there is ample evidence of relatively short foraging migrations of reef organisms into seagrass areas in the form of grazed halos of bare sand several meters wide between reef and vegetated habitats (Ogden 1976; Ogden and Zieman 1977; Tribble 1981). Broader scale interactions between reef and adjacent sand and seagrass habitat occur in the Haemulidae (grunts) and Mullidae (goatfishes) which utilize the reef as a structural refuge and migrate 10-100's of meters into sand and seagrass areas to forage (Randall 1967; Helfman et al 1982; Burke 1995; Randall 1996). Other species that cruise higher in the water column are even more wide ranging, with daily travels encompassing many different habitat types (Grober-Dunsmore et al. 2007). There are also indirect influences on the distribution of other organisms through a web of ecological pathways. More sedentary species may interact indirectly with adjacent habitats through flux of materials such as nutrients or even as a secondary effect of the movements of wider ranging organisms (Meyer et al 1983, Meyer and Shultz 1985). In addition, some predatory reef fish have been observed to position themselves along regular migration corridors (Helfman et al 1982). Differences in intensity of piscivory have also been documented based on location on a reef (Connell 1996; Letourneur 1996) or distance from reefs (Shulman 1985). Only by evaluating the structure of a local fish

assemblage in the context of its position relative to adjacent elements in the marine landscape can a more complete understanding of the spatial influences on ecosystem structure be achieved (Irlandi and Crawford 1997).

Does map resolution influence the perception of correlations between fish assemblages and their landscapes?

To fully understand the issues introduced above, it is also necessary to explore the influence of the characteristics of the source data, or habitat maps, on the relationships that can be detected between fish assemblages and their landscapes (Syms 1995; Karl et al 2000). Most landscape ecology studies linking organisms to habitat use only one map type: whatever is available! The spatial resolution, minimum mapping unit (MMU), and level of categorical detail in the classification scheme of habitat maps could limit the types of fish/habitat associations that can be identified. Correlations between fish and their associated reef or landscape elements should be calculated using different types of benthic maps and compared. Comparing such results reveals the consequences, if any, of using a particular map type and how perception of a fish-habitat relationship may change as a result of the spatial and thematic characteristics of input maps. Do fish use benthic maps when deciding where to live? No, but we rely on them when trying to predict it.

Platform for Analysis

The study area for this dissertation is located off of St.Croix, the largest of the United States Virgin Islands. The northeastern insular shelf of St.Croix is the site of two marine protected areas (MPA), the Buck Island Reef National Monument

(BIRNM) which is administered by the National Park Service, and the adjacent East End Marine Park which is a Virgin Islands Territorial Park (Figure 1.1). The data for the dissertation were collected in the ~50 km² reef ecosystem partially overlapping these two MPAs.

Three types of data were used in the analyses; benthic maps, fish surveys, and fine-scale benthic characterization that accompanied each fish survey. Two maps of the benthic landscape were produced, one with a large (4048 m²) and the other a small (100 m²) minimum mapping unit. The classification scheme for these maps was hierarchical with a total of 15 subcategories nested within 3 major categories. The major categories were unconsolidated sediment, submerged vegetation, and coral reef/hard bottom. These maps were the basis of the landscape scale analyses.

Visual surveys were used to census the fish community at 588 sites in the study area between January 2002 and May 2006 (Figure 1.1). The methods and sampling design for this ongoing dataset were devised specifically to assess and monitor the reef ecosystem in and around BIRNM (Pittman et al. 2008). To date, these data have been used to evaluate the abundance and size structure of local fish communities under different management regimes. As one of the main architects of the stratified random sampling design described below, I sought to ensure that the sampling strategy yielded additional opportunities for analysis beyond the monitoring objectives for which the protocols were primarily designed. Prior to data collection, I devised the landscape analyses that combined map, benthic, and fish data that are presented in this dissertation. During the design phase of the monitoring program I ensured that the fish survey data would specifically support a test of landscape

hypotheses while also meeting their primary goal of BIRNM monitoring. Additional details on the methods and objectives for which the sampling strategy was designed are provided in Pittman et al. (2008). Samples were randomly located within several spatial strata; hard bottom or soft bottom, inside or outside lagoons, and inside or outside BIRNM. This monitoring design resulted in sample sites being spread widely throughout the benthic landscape with each sample site surrounded by a unique combination of habitat elements. In addition, unlike many reef studies and monitoring programs, the full diversity of reef types in the study area was included in the program. The dissertation utilized this diversity of landscape combinations around the hundreds of independent surveys of the fish assemblage to identify relationships between the distribution of fish, local habitat variables, reef types, and landscape patterns. This suite of analyses is entirely independent of the analyses conducted for BIRNM monitoring.

At each survey site, a diver secured a 25 m tape reel to the substrate and then swam along a randomly selected compass heading until the tape was completely unreeled. While swimming, the diver recorded all fish observed within 2 m of both sides of the transect to the lowest possible taxon, their abundance, and estimated fork length within 5 cm size classes. I personally conducted ~200 of the fish surveys used in these analyses. In addition to the census of the fish community, fine-scale habitat metrics such as rugosity and percent cover of specific bottom characteristics were recorded along the transect for each site.

Dissertation Structure

Description of Chapters

This dissertation is separated into five chapters. Chapters 1 and 5 introduce and summarize the dissertation respectively. The core chapters, 2-4, test interrelated hypotheses regarding the landscape ecology of coral reefs and the benthic maps that are used to study them. The core chapters have been written in a style and format for submission to scientific journals. Here I describe the central objective of each chapter, how they related to the general theme of the dissertation identified in the Statement of Problem. Each chapter summary ends with an indication of which journal the work is targeted for. It is intended that several of the chapters will be published as co-authored articles. Under such circumstances it is important that a clear statement is made of the contribution that each author has made to the work. In accordance with the above, I provide the following summary.

Chapter 1: Dissertation Introduction. This chapter is entirely my own work. It is not expected that this material will be submitted for publication.

Chapter 2: The influence of thematic and spatial resolution on maps of a coral reef ecosystem. This chapter has been accepted for publication in the journal Marine Geodesy. It reflects collaboration between myself and my advisor, Dr. Thomas Miller. The conceptual foundations of the chapter were my own. Dr. Miller's contribution was not anything beyond what might be expected from an advisor in terms of editorial and statistical advice.

Chapter 3: Relationships among fish assemblages, habitat variables, and benthic maps. This chapter will be submitted to a marine ecology journal such as Marine

Ecology Progress Series or Bulletin of Marine Science. Similar to Chapter 2, it reflects collaboration between myself and my advisor, Dr. Thomas Miller. The conceptual foundations of the chapter were my own. Dr. Miller's contribution was not anything beyond what might be expected from an advisor in terms of editorial and statistical advice.

Chapter 4: How big are fish scales? This chapter will be submitted to a journal strong in spatial ecology. Because it is lengthier than the typical journal article it will be submitted to Ecological Monographs. Other alternatives include shortening the material and submitting to a more focused topical journal such as Landscape Ecology, with a refocus on the spatial analyses and method, or Coral Reefs, with a refocus on reef organisms.

Chapter 5: Summary and Conclusions. This chapter is entirely my own work. It is not expected that this material will be submitted for publication. The objective of Chapter 5 was to summarize the main findings from each of the individual chapters and integrate them into a brief discussion of key results. In addition, comments on how the study design could have been improved and recommendations for future research are provided.

Contribution of Core Chapters

Chapter 2: Published as *Kendall, M. S. and T. J. Miller (2008). The influence of thematic and spatial resolution on maps of a coral reef ecosystem. Marine Geodesy 31: 75-102*

The primary objective of Chapter 2 was to quantify the differences in perception of coral reef landscapes depending on map scale. Specifically, the

influence of spatial (size of mapped features) and thematic (number of classified reef types) resolution was examined through landscape parameters for each of the map conditions in Figure 1.2.

Among the first steps necessary in identifying the influences of the landscape on fish distribution is achieving an understanding of the spatial characteristics of the landscapes with which they interact. Individual fish sense and respond to landscape cues through a variety of mechanisms, however, we can only perceive the fishes regional landscape through the limited lens of remote sensing. Analysis of the spatial configuration of the landscape elements that we can perceive may offer insight into the types of variables that fish respond and distribute themselves in relation to. Comparison of differences in landscape metrics that are based on maps with different MMUs and levels of categorical detail could reveal how each of the maps may be limited in predicting fish distributions.

The goal in selecting specific metrics for analysis in this chapter was to obtain a general understanding of the differences among maps and be as broadly descriptive as possible without redundancy. First, geospatial metrics that described general map characteristics for each of the four map conditions in Figure 1.2 were calculated. For each map category polygon area, perimeter, shape index, nearest neighbor, and other metrics of landscapes such as number of polygons, diversity, and proportion of each map category were calculated. A combination of non-parametric and re-sampling statistical techniques were used to compare values among map types and categories. These maps and many of the differences quantified among them were the basis for the analyses in Chapters 3 and 4.

Chapter 3: Intended to be published as *Kendall, M. S. and T. J. Miller.*

Relationships among reef fish assemblage, local environment, and benthic maps.

The primary objective of Chapter 3 was to determine if the reef types depicted in benthic maps represented discrete and predictable reef fish assemblages and fine-scale environmental characteristics.

Analyses in this chapter were focused at the scale of the landscape patch. Fish assemblage and benthic data from the scuba survey sites were subjected to multivariate analyses to determine if sites could be meaningfully clustered to represent particular reef types. More importantly, the patch type that each survey took place in according to the benthic maps was subjected to discrimination analyses to determine if they represented specific fish assemblages or benthic types. The goal of these analyses was one of prediction for the entire fish community rather than individual species or guilds. As suggested by Chapter 2, analyses were conducted using the different benthic maps as inputs and the results were compared.

Chapter 4: Intended to be published as *Kendall, M. S. and T. J. Miller. How big are fish scales?*

Landscape analyses in Chapter 3 were constrained to patch type. Chapter 4 broadened the scale of analysis and looked beyond the patch in which each survey took place, to consider the influence of surrounding landscape features on fish assemblages. The primary objective of Chapter 4 was to identify the scale with which fish are most correlated with their surrounding habitat elements.

To determine how the fish assemblage at a given location is influenced by surrounding habitats, correlations between fish population metrics and landscape parameters were systematically explored across a range of scales. In contrast to Chapter 3, in which the entire fish assemblage was considered in multivariate analyses, fish variables in Chapter 4 were analyzed using a univariate but hierarchical approach beginning with abundance of individual life stages of single species, then all life stages, then groups of species with similar mobility, and finally using the assemblage-level metrics of species richness and total abundance.

The value of a landscape metric at a given site depends on the size of the area around that site that is considered during the measurement. In this chapter, landscape metrics were calculated for each fish survey site at a range of distances. This included the extremely fine-scale associated with the habitat only directly at the survey site, through broad scales that incorporate both the local habitat and the mosaic of habitats beyond the distance that fish are likely to be influenced.

The strength of the correlation between a given parameter of the fish community and a landscape parameter was calculated for each of the distances that landscape metrics were produced. Once correlations were established across the range of scales, the strength of the associations were examined to find the “scale of best prediction” between the fish and its habitat. Landscape metrics that incorporate too much or too little habitat (analysis window too large or too small respectively) will have less explanatory power and hence lower correlation than metrics calculated using only the area of habitat that is most influential on that particular parameter of the fish assemblage. As with Chapter 3, the influence of map types on the value of

landscape variables and in turn the results of the fish-habitat scale predictions were considered.

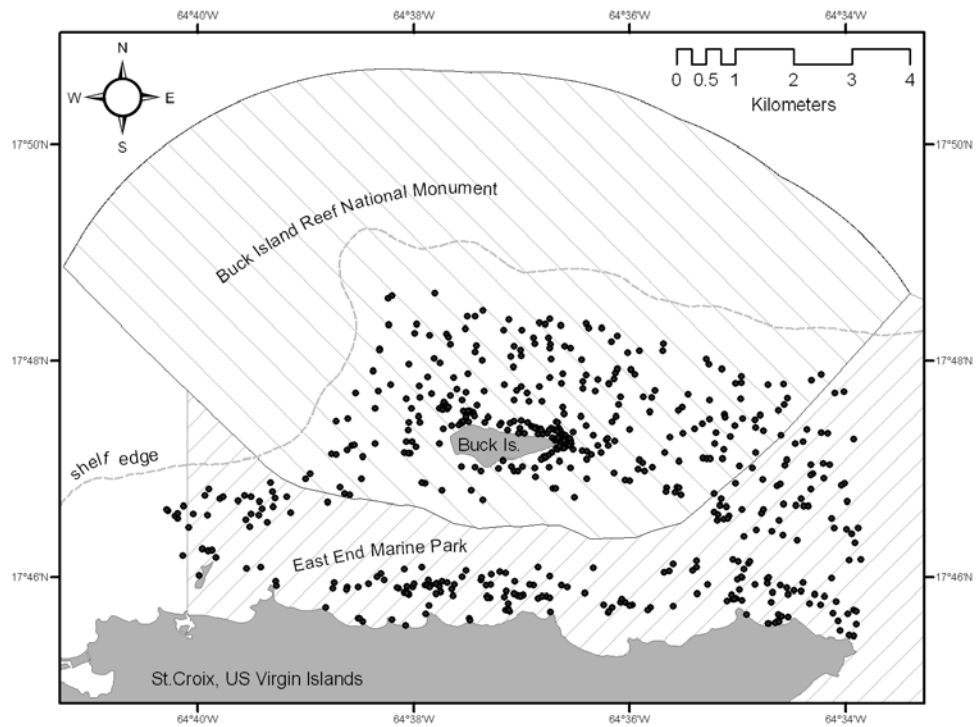
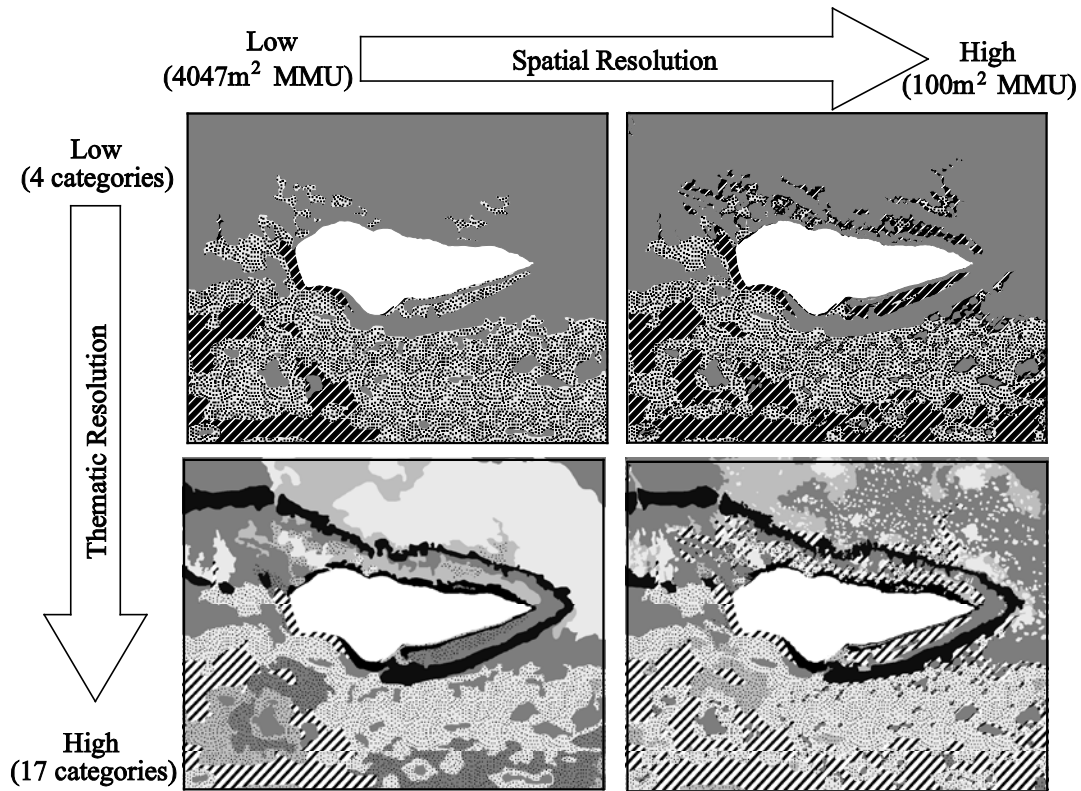


Figure 1.1: The study area around Buck Island, St.Croix. Dots denote the location of field surveys.



Chapter 2: The influence of thematic and spatial resolution on maps of a coral reef ecosystem.

Abstract

Benthic maps are essential tools for marine scientists and managers. Map characteristics are controlled by the spatial and thematic resolutions selected during map production. However, the implications of these production decisions on the inferences that can be drawn from the maps are poorly quantified and understood. To address this need, four maps of a coral reef ecosystem were created using two levels of both spatial and thematic (number of classifications) resolution. Differences among maps were quantified using indices from the field of landscape ecology. The results indicate that inferences regarding the structure and organization of reef ecosystems are sensitive to changes in spatial and thematic resolution of the maps characterizing them. Significant differences were found for 28 out of 44 comparisons among independent bottom types and landscape metrics. Increasing thematic resolution greatly increased the number of map polygons, total edge length of polygons, and the diversity of maps by splitting the landscape into more categories. Changing the spatial resolution (minimum mapping unit) resulted in disproportionate changes in bottom types for nearly all metrics considered. When spatial resolution was increased by mapping smaller features, dominant bottom types such as hard bottom became less dominant and rare bottom types became more common. For metrics based on whole maps, the range of values observed in total number of polygons, average feature size, and total edge spanned an order of magnitude among

maps. For individual bottom types, hard bottom in general, especially the patch reefs and colonized pavement components, as well as sand areas and patchy features were among the most sensitive to change in spatial resolution. In contrast, linear reef and continuous seagrass features were characterized quite consistently regardless of spatial resolution used in mapping. The findings demonstrate that the spatial and thematic resolution of benthic maps imposed during their creation must be carefully considered and understood. Results of ecological studies or recommended management actions can vary considerably depending on the thematic and spatial characteristics of the map used as input.

Introduction

Marine scientists and managers are increasingly relying on maps of benthic cover and ecosystem scale analyses to support their activities. Maps can be characterized by two properties: their spatial and thematic resolution. Spatial resolution is typically given as the minimum mapping unit (MMU) which often corresponds to the pixel size or grain of raster or grid based maps and the area of the smallest mapped feature in a vector or polygon based map. Thematic resolution is defined as the amount of categorical detail in a map. Thematic resolution is typically given as the number of feature types, classes, or themes. A variety of remote sensing technologies and processing techniques are available for creating maps of the benthic landscape. Each approach produces maps with different spatial and thematic characteristics. The scale of aerial photography, pixel size of remotely sensed data, spectral sensitivities of film and sensors, as well as processing steps following image acquisition all limit the potential spatial and thematic resolution of map products.

Understanding quantitative differences among maps of different spatial and thematic resolution as measured through landscape metrics such as average feature size, shape, and connectivity is crucial when selecting from the variety of available remote sensing technologies and processing techniques to ensure that maps meet the requirements of a given application, (Benson and MacKenzie 1995, Mumby et al. 1997, Saura 2002).

Map characteristics, primarily the biases and limitations associated with different levels of spatial and thematic resolution, have been shown to directly influence the results of ecological studies. For example, Stohlgren et al. (1997) resampled a vegetation cover map across a range of MMUs (0.02 to 100 ha) and estimated the number of plant species in the landscape by using species-area curves from field surveys combined with the number and area of polygons in each resampled map. They found that the use of large MMUs dramatically underestimated overall plant community diversity, the number of habitat patches, and total plant species richness. They estimated that the total estimated number of plant species was 35% lower for the largest MMU considered (341 species) relative to the smallest MMU (522). Karl et al. (2000) provide a second effective terrestrial example of how both spatial and thematic resolution of landscape maps can influence the results of ecological studies. Karl et al. (2000) modeled habitat relationships for birds based on landscape slope, vegetation type, and canopy closure. These map variables were resampled at three spatial resolutions (0.09, 4, and 10 ha) and two hierarchical levels of thematic complexity. Their results varied according to model complexity (amount of habitat information) and the level of spatial and thematic resolution of input maps.

Models predicting bird distribution using maps with fewer thematic categories generally performed better than those using many themes. When simple models were used, there were few differences in model performance based on spatial resolution but when complex models were used, results based on maps with high spatial resolution were better than those based on coarse resolution. The extent to which the results of such studies can be generalized to other systems is unknown.

Maps are also increasingly used to support management actions such as selection of marine protected areas (MPAs)(St.Martin 2004). Understanding the influence of spatial and thematic resolution of maps on such decisions is a crucial component in their successful application. A good example of how spatial and thematic properties of benthic maps might influence a process to create a network of MPAs in the Florida Keys was recently provided by Leslie et al (2003). Among the objectives of their analyses was the identification of possible MPAs that protected 20% of all habitat types while minimizing the area and perimeter of the resulting MPAs. They converted benthic map data from polygon format into grids of two different resolutions (1 and 100 km²) and also examined the effect of using high (26 categories) versus low (6) thematic resolution. Each grid cell was characterized by the percentages of each bottom type in the original, polygon based map. While this is not the same as resampling the MMU it does offer an example of how spatial resolution of map data influences analytical conclusions. Their results indicated that the total area needed to meet MPA objectives differed dramatically depending on the grid size and number of themes used to conduct the analysis. In the most extreme contrast, the best MPA option based on high thematic and low spatial resolution maps

required nearly twice as much area to meet study objectives compared to results based on low thematic and high spatial resolution maps.

Of more pragmatic concern than the analytical and management issues discussed in the examples above, maps with more spatial and categorical detail are generally more time consuming and more expensive to produce than simpler maps (Mumby et al. 1997). Because of funding and logistical constraints it is important to understand the minimum level of spatial and thematic detail needed to meet research or management objectives (Stohlgren et al 1997).

Most investigations of the influence of spatial and thematic resolution on map characteristics have been conducted based on terrestrial systems (Turner et al. 1989, Benson and MacKenzie 1995, Wickham and Riitters 1995, Cain et al. 1997, Wu et al. 2002, Lioubimtseva 2003, Manson et al. 2003, Neel et al. 2004, Saura 2004), a limited number of studies have explored the impact of scale using neutral models (computer generated landscapes; Turner et al. 1989, Saura 2002, Neel et al. 2004, Shen et al. 2004), and very little has been attempted in the marine realm (but see Andréfouët et al. 2003 and Prada et al. 2008). Turner et al. (1989) were the first to investigate the effects of changing spatial resolution and map extent on simple landscape metrics using neutral models and by resampling land cover maps. They found that as spatial resolution became coarser, that is grain size is increased, rare map categories were lost and dominant categories became more dominant. The rate of change depended on patchiness of the landscape with clumped distributions of rare landscape features being lost more slowly when grain was increased whereas patchy distributions were lost more quickly. Saura (2002) used a more extensive series of

computer generated artificial landscapes to investigate the effects of MMU and fragmentation on 10 landscape indices. Their results confirmed the findings of Turner et al. (1989) and also found that 1) diversity and fragmentation indices tended to be underestimated when larger MMU was used whereas dispersal can be overestimated, 2) total edge length decreased with larger MMU, and 3) mean shape index was highly sensitive to changes in MMU, increasing significantly with larger MMU.

Studies on real landscapes have generally confirmed the results of the above, primarily computer simulation studies. A number of researchers have compared landscape metrics from different land cover maps of a given site. Maps in these studies may be derived from a variety of satellite sensors with different spatial resolutions (Benson and MacKenzie 1995, Saura 2004) or more often are created by aggregation of data, through resampling of high resolution data, into larger MMUs (typically ~10 m through >1000 m pixel sizes depending on the study) (Turner et al. 1989, Benson and MacKenzie 1995, Wickham and Riitters 1995, Cain et al. 1997, Wu et al. 2002, Lioubimtseva 2003, Manson et al. 2003, Saura 2004). The results of these studies largely uphold those of Turner et al. (1989) and show that as grain size or MMU is increased, rare cover types become even more rare and dominant cover types become more dominant (Benson and MacKenzie 1995, Stohlgren et al. 1997, Lioubimtseva 2003; but see Wickham and Riitters 1995 who used a small range of pixel sizes relative to other studies).

Previous investigations of the effects of spatial and thematic resolution on inferences drawn from maps of marine or benthic landscapes are quite rare despite a

recent surge in benthic mapping capabilities (but see Andrefouet et al. 2003 and Prada et al. 2008). Coral ecosystems in particular provide attractive model systems for such studies for three primary reasons. First, tropical marine, or coral reef ecosystems are patchy landscapes with diverse bottom types including a variety of sand, submerged vegetation, and hard bottom features. The complex ecological interactions among these bottom types have been only recently explored using landscape ecological theory. Second, these bottom features are often arranged and shaped predictably according to their geological, ecological, and environmental context although their spatial properties have not been systematically quantified. Third, coral ecosystems principally occur in shallow, clear water which means landscape scale benthic maps can be produced from remote sensing or aerial photography and are increasingly available for many regions.

Andréfouët et al. (2003) provide a rare examination of issues in maps of coral ecosystems. They examined the influence of the spatial resolution (5 to 1100 m pixel size) of four commonly used satellite sensors on landscape parameters for atolls in French Polynesia. The metrics considered were highly specialized for atoll characterization and do not transfer readily to prior terrestrial or neutral modeling studies. Nevertheless, their results indicated that the values of most atoll metrics were sensitive to the spatial resolution of remotely sensed data. Despite this good first step, the influence of map characteristics on more mainstream landscape indices remains a largely unexplored topic for tropical marine ecosystems.

Here, I apply commonly used landscape metrics for the first time, to study the influence of spatial and thematic resolution on properties of benthic maps of a coral

reef ecosystem. Characteristics of four different benthic maps were quantified through selected landscape parameters for each of the map conditions; high thematic and spatial resolution, low thematic and spatial resolution, high thematic but low spatial resolution, and low thematic but high spatial resolution (Figure 2.1).

Particular attention was given to landscape elements that are typical of and unique to reef ecosystems and how they may influence the value of landscape indices. Some prominent features typical of coral ecosystems include: 1) linear barrier and fringing reef formations that are usually narrow and oriented parallel to the shore line and shelf edge, 2) a thin band of hard bottom adjacent to land which is usually merely an extension of the terrestrial bedrock although its often colonized by corals and macroalgae, 3) numerous roughly round patch reef formations that are isolated from each other and other reef formations to varying degrees, 4) “spur and groove” formations composed of alternating hard bottom and sand channels typically oriented perpendicular to the dominant wave surge, 5) seagrass and macroalgal meadows of varying degrees of patchiness which typically occur in low wave energy environments such as bays or lagoons, 6) sand fringe or “halo’s” between reefs and seagrass beds, and 7) mangroves that often fringe protected shorelines.

There are additional notable differences between the approach used in this study and most previous studies. Most prior investigations into this topic rely on landscape indices generated based on whole maps. Whole map metrics yield a single value for an entire map and generally result from taking the grand mean of some metric calculated separately for each polygon in a given map (e.g. average polygon size). Consequently such studies ignore what is often a wide distribution of values

representing individual polygons and are limited to discussion of qualitative rather than statistical comparisons between maps. Instead, by calculating metrics and comparing maps based on the range of values for all of the individual polygons of a given type (without averaging all the individual values), statistical differences in maps and feature types can be identified and a better understanding of the distribution of values for all polygons in the landscape is obtained. Also of note, most previous studies resample some original high resolution map into increasingly coarser pixel sizes as the basis for comparisons rather than independently creating maps with different spatial resolutions. When the same map is resampled to create comparison maps, the rules governing the resampling process can potentially dictate or at a minimum bias the results (Saura 2004). Saura (2004) demonstrated that spatial aggregation using majority rules, for example, can produce more fragmented patterns than maps produced from satellites with differing spatial resolution (see Benson and MacKenzie 1995 and Bian and Butler 1999 for additional discussion). To avoid this potential problem in this study, maps with high or low spatial resolution respectively were produced independently for comparisons.

My objectives were to 1) compare coral ecosystem maps produced with two commonly used spatial and thematic resolutions, 2) quantify and statistically identify significant differences among maps and categories with frequently used indices from the field of landscape ecology, 3) examine the relative sensitivities of common features of coral ecosystems to detection by each spatial and thematic resolution considered, and 4) identify how typical features of the coral reef ecosystem influence

the behavior of landscape metrics at different levels of spatial and thematic resolution.

Methods

The coral reef ecosystem off northeastern St. Croix, U.S. Virgin Islands was the focus of the study (Figure 2.2). The study area extended from Green Key eastward including the insular shelf around Buck Island to Point Udall and covered approximately 50 km². Two maps of the benthic landscape of this area were produced; one using a relatively large MMU of 4047 m² (1 acre), the other a much smaller MMU of 100 m² (0.0247 acre). Both maps were visually interpreted from the same orthorectified photomosaic using quite similar hierarchical classification schemes and digitizing software (Kendall et al. 2001). In this technique, image tone and texture representing specific bottom types are delineated and labeled with the aide of a geographic information system. Additional details on the methods used for map production are available in Kendall et al. (2001).

The original classification schemes used to create these maps differed slightly in a few subcategories such that some map themes and features were combined to make all map features and categories directly comparable. First, only two categories of patchy seagrass and macroalgae (10-50 and 50-90 % cover respectively) were used to create maps with small MMU whereas four categories (10-30, 30-50, 50-70, and 70-90) were used to produce maps with large MMU. To make maps comparable, the four categories of patchiness used in the large MMU map were reduced to two and polygons were combined as appropriate. For example, where a 10-30% patchy

seagrass polygon was adjacent to a 30-50% polygon, features were combined into a single polygon attributed with 10-50% cover. Similarly, the map produced with the small MMU did not have the “aggregated patch reefs” category which was used in the large MMU map to delineate groups of patch reefs that were too small to delineate individually but were collectively larger than the MMU. To make maps comparable in this category, small single or aggregated patch reef polygons of both maps were relabeled merely as “patch reef (s)”. Also, the “colonized pavement with sand channels” category was only used in the map with large MMU, therefore those polygons were reclassified as merely “pavement” to improve map comparability. Also, both scales of map were originally produced using both colonized and uncolonized classes of bedrock and pavement. Due to the extreme rarity of uncolonized bedrock and pavement in both maps and when present their position adjacent to or encompassed by larger colonized neighbors, these polygons were merged and attributed simply as colonized pavement and colonized bedrock respectively. Last, an additional hierarchical level of subcategories was used in production of the map with small MMU such as dominant species of seagrass. These subcategories were simply aggregated upward to match categories from the large MMU map which did not have species level information. No modifications were necessary at the highest level in the classification hierarchy.

The resulting slightly restructured classification scheme used to attribute maps at both spatial scales remained hierarchical and included a total of 17 subcategories nested within the following 4 main categories; unconsolidated sediment, submerged vegetation, hard bottom, and other (Table 2.1). The maps with 17 classes served as

the high thematic resolution. These maps then had boundaries dissolved and polygons aggregated to the 4 thematic class level for use in the analyses as maps with low thematic resolution. This process resulted in four maps of the same area using the same approach but with different spatial and thematic characteristics (Figure 2.1).

The field of landscape ecology has generated a tremendous variety of metrics that can be used to quantify map characteristics (Haines-Young and Chopping 1996, Gustafson 1998). There are two general types of metrics, those that evaluate composition of a map and those that evaluate the spatial configuration of map elements (Gustafson 1998). Composition metrics include simple descriptive parameters including number of patches, proportion of patch types, and diversity indices. Spatial configuration metrics are either based on the shape of individual patches or the relative proximity of patches to each other. There are many closely related landscape metrics within each of these categories (Haines-Young and Chopping 1996) that yield highly correlated results (Riitters et al. 1995). The goal in selecting specific metrics for analysis in this study was to obtain a general understanding of the differences among maps and be as broadly descriptive as possible without redundancy. Therefore, a minimum set of independent metrics of each type were selected that would be broadly interpretable and provide a general understanding of the differences among four map conditions under consideration. Other metrics should be used to investigate and test hypotheses regarding specific ecological processes.

The landscape metrics evaluated began with simple descriptive measures before more complex landscape indices were considered. First, general metrics were

calculated that describe whole map characteristics for each of the four map conditions in figure 2.1. Metrics calculated for each map include total number of polygons, average polygon area, and sum of all polygon perimeters. In addition, mean shape index (MSI), mean nearest-neighbor (MNN) distance, and Simpson and Shannon diversity based on number and then area of patches were also calculated. The formulas for each metric are as follows:

$$MSI = \frac{\sum \left(\frac{0.25p}{\sqrt{a}} \right)}{N}$$

...where p is polygon perimeter and a is polygon area - the shape index of a perfect circle has a value of ~0.9 whereas a perfect square equals 1 and shapes with more complex edges will have even higher values.

$$MNN = \frac{\sum d}{N}$$

...where d is the distance from a polygon to its nearest neighbor (NN) of the same polygon type.

Simpson Index (1/D) is calculated as...

$$\frac{1}{\sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right)}$$

...where n_i is the number (or area) of polygons in the i th class and N is the total number of polygons.

Shannon Index (H') is calculated as...

$$-\sum \left(\frac{n_i}{N} \right) \log_{10} \left(\frac{n_i}{N} \right)$$

During interpretation it is useful to note that the Shannon index achieves a maximum value when map features are equally distributed among classes. Values are 0.45 and 1.23 when four and seventeen map classes respectively are equally distributed. Both the Shannon and Simpson indices were used since they can differ in sensitivity to changes in rare (Shannon) versus common (Simpson) features.

Next, comparisons among bottom types and between maps with different MMUs but the same level of thematic resolution were conducted. The number of polygons, total perimeter, and percentage of the total map area represented by each bottom type were determined. The number and length of edge types were also examined. For maps with only 4 classes the number of edges, total edge length, and mean edge length of all paired combinations of hard bottom, unconsolidated sediment, and submerged vegetation were considered. For maps with 17 categories a total of 136 paired edge comparisons are possible, therefore only a subset of key edge types were examined. Selection was based on preliminary results from other analyses that indicated which edge types would be notably affected by MMU changes as well as ecological processes known to occur across particular edge types in coral ecosystems that would be of interest to scientists and managers. Selected edge types for high thematic resolution maps included linear reef-sand, linear reef-continuous seagrass, patch reef (s)-sand, patch reef (s)-continuous seagrass, colonized pavement-

sand, colonized pavement-patch reef (s), and colonized pavement-continuous seagrass.

The above metrics result in an average or total value for each map that is based on all map elements. While useful in providing general descriptive results between maps, single valued metrics do not allow statistical comparisons to be made and ignore the variability represented by the range of individual polygon values, an important but often overlooked component of describing the landscape. To better understand the distribution of individual polygon sizes, shapes, and configurations within and among bottom types for each map, the area, perimeter, shape index, distance to nearest neighbor, and edge length values for each individual polygon or edge in the maps were treated as samples as the basis for statistical comparisons. For example, a map with 100 patch reefs would have 100 observations for each metric. The distribution of values for these variables did not conform to the assumptions of parametric analysis and could not be transformed to do so. Therefore, Monte Carlo resampling was used to determine if mean values of landscape metrics differed significantly among bottom types and MMU levels. First, the mean and sample size (number of polygons or edges) of every MMU/bottom type combination were calculated for polygon area, perimeter, nearest neighbor, shape index, and edge length. All possible pairwise differences between means were then calculated. The probability that the result of each pairwise comparison could have resulted from random chance was calculated. For each pairwise comparison, polygon values from both groups were pooled. Data were randomly regrouped into the same sample sizes as the original two groups and the mean for each regrouping was calculated. Next, the

difference of the two resampled means was calculated and compared to the difference in means of the original two groups. This procedure was repeated 10,000 times to calculate the proportion of times the difference of the randomly resampled means was equal to or greater than the difference of the original two means. This proportion served as a p-value for a test of the hypothesis that a difference between means as big as that observed difference between the actual means would be expected by chance alone. Results of all pairwise comparisons are presented in matrix format for each metric. P-values less than 0.05 were considered significant differences (the difference in the original means happened merely by chance less than 5% of the 10,000 resampling runs). Conducting so many pairwise tests increased the probability that any one result could have occurred by chance alone. Therefore, general patterns are discussed and caution should be used in the interpretation of individual p-values. In addition, a protected, non-parametric test (Dunn's multiple comparison), was also used and yielded very similar results. Only MMU/bottom type combinations with a minimum sample size of 10 features were included in these analyses. Polygons in the 'other delineations' category were necessary for map production but were not considered in the analyses or figures since they were few in number and were not the primary focus of this study.

Results

Whole Map Comparisons

The number of polygons ranged from 113 for the map with low thematic and spatial resolution to 2497 for the map with the high spatial and thematic resolution

(Table 2.2). Average feature size ranged from 51.4 ha for the most general map to only 2.3 ha for most spatially and thematically detailed map. The sum of all edges for the map with low spatial and thematic resolution was the shortest at 225 km. Total edge lengths were twice as long, ~450 km, for both the map with large MMU and high thematic resolution, and the map with small MMU and low thematic resolution. The map with both high spatial and thematic resolution had the highest total edge length of 790 km.

The results of the diversity analyses yielded similar patterns among maps regardless of the metric used (Shannon or Simpson) or the basis of the calculation (number or area of polygons) (Table 2.2). Comparisons of diversity values are most meaningful when considered for maps with similar levels of thematic resolution (maps with many categories simply had much higher diversity than those with fewer categories). The map with few thematic categories and small MMU had slightly higher diversity than the map with few themes but large MMU. In contrast, the map with many thematic categories and small MMU had slightly lower diversity than the map with many themes but large MMU.

MSI was highest for maps with larger MMU (Table 2.2). MNN distances for maps with large MMU were three times farther than those with small MMU and the same number of categories. When maps with the same MMU were compared, increasing the number of categories only increased the MNN distance slightly.

Comparisons among Maps and Bottom Types Produced with Low Thematic Resolution

When maps with only four classifications but different MMUs were compared, disproportionate changes among bottom types were observed for nearly all metrics. When MMU size was smaller, the number of polygons increased in each bottom type, but not in equal proportions (Figure 2.3). In maps with the smaller MMU, there were approximately 8 times more hard bottom polygons (582 vs. 71 mapped features), and 10 times more submerged vegetation polygons (159 vs. 15 mapped features) than in maps with large MMUs. A much larger increase of ~15 times more polygons were mapped in the unconsolidated sediment category (133 vs. 19 mapped features) when the MMU was smaller.

Total perimeter by bottom type also increased with smaller MMU size for all categories although increases were not equal among classifications (Figure 2.4). The perimeter of soft bottom polygons went from the smallest to largest total length, 54 to 314 km, when the MMU size was reduced. Proportional area covered by each of these bottom types differed as well depending on MMU (Figure 2.3). When MMU size was smaller, the total area of hard bottom and submerged vegetation decreased whereas the area of unconsolidated sediment increased.

With few exceptions MMU size had a significant effect on mean polygon size, perimeter length, shape index (SI), and NN values for all bottom types (Tables 2.3-2.6). In the Monte Carlo sampling tests comparing mean values, hard-bottom values mapped with small versus large MMU were significantly different from each other in all four landscape metrics tested (Table 2.1). When mapped with small versus large MMU, submerged vegetation values were significantly different from each other in

two of the four metrics considered and nearly so for a third ($p=0.07$ for nearest neighbor). Unconsolidated sediment values were significantly different in only one metric although p -values for two others were nearly significant at 0.06 and 0.07 for area and perimeter respectively (these categories were further evaluated with Dunn's non-parametric multiple means test based on ranks and found to be significantly different, $p<0.05$).

Also of note, mean landscape metrics of hard bottom polygons mapped with the small MMU were the smallest of all the MMU/bottom type combinations (except area for which it was the second smallest) and were often significantly lower than all other bottom types regardless of MMU. In addition, mean SI and NN values of unconsolidated sediment polygons mapped with the small MMU were the largest of any category regardless of bottom type or MMU, counter to the general trend of smaller values for smaller MMUs (Tables 2.5-2.6) observed for other bottom types.

The distribution of edge types also differed between maps with large or small MMU (Table 2.7). When the large MMU was used, edges between hard bottom and submerged vegetation polygons were dominant over other edge types both numerically ($n = 90$ or 70% of edges) and in total length (121 km or 72% of total edge length). In marked contrast, when the smaller MMU was used, edges between hard bottom and submerged vegetation became the least common type (both numerically and in total length). Instead, when the smaller MMU was used, hard bottom/unconsolidated sediment edges dominated numerically ($n = 634$ or 64% of edges) and in total length although total edge length exhibited a more equitable distribution among edge types (167 km or 41% of total edge length, the next most

common edge type was 32% of the total). Mean edge lengths were significantly longer for all edge types when the larger MMU was used. Edges between unconsolidated sediment and hard bottom when the small MMU was used were significantly smaller than the rest of the edge types regardless of MMU.

Comparisons among Maps and Bottom Types Produced with High Thematic Resolution

Maps with 17 classifications but different MMUs also exhibited disproportionate changes among bottom types for nearly all metrics. A notable exception was the linear reef category which exhibited no significant changes in any parameter when the different MMUs were used. Despite this exception, when MMU was smaller, the number of polygons increased in all categories, but not in equal proportions (Figure 2.5). Notable increases included 16 times more sand, from 19 to 312 polygons, and 40 times more patch reef (s) polygons (18 to 770). Also of note, four new patch types which did not exist in the large MMU map appeared when the smaller MMU was used. New types included artificial and macroalgae in varying degrees of patchiness.

Total perimeter by bottom type also increased with smaller MMU for nearly all categories, although increases were not equal among classifications (Figure 2.6). The combined perimeter of sand polygons exhibited the greatest total and proportional increase from 50 to over 300 km. Only very patchy seagrass (10-50%) lost a large proportion of its perimeter when the smaller MMU was used.

Proportional area covered by each of the bottom types differed as well depending on MMU although big changes in area were only observed for a few

categories (Figure 2.7). Very patchy (10-50%) seagrass and patch reef (s) both lost total area whereas sand gained considerably covering nearly three times more area (from 260 to 797 hectares) when a smaller MMU was used.

Twenty combinations of bottom type and MMU had sufficient sample size to allow statistical comparisons between means through Monte Carlo sampling. The general pattern in mean polygon size, perimeter, SI, and NN values was for significantly higher values to be observed for bottom types mapped with the larger MMU (Tables 2.8-2.11). Comparisons within each bottom type indicated that linear reef features were insensitive to changing MMU in all four landscape metrics considered (Table 2.1). Continuous seagrass features were significantly different in only nearest neighbor values when different MMU was used. More affected by MMU, sand and colonized pavement showed moderate sensitivity, with significant or nearly significant differences in three of the four metrics evaluated. Most sensitive to MMU were patchy seagrass categories, patch reef(s), and scattered coral and rock in sand which were very sensitive to MMU showing significant differences in all four metrics considered. Consistently at the lowest end of the spectrum of values for all metrics were patch reef (s), colonized pavement, and 10-50% patchy seagrass mapped with small MMU, almost always significantly lower than other combinations of bottom type and MMU (Tables 2.8-2.11).

The dominant edge types among those considered also differed between maps with large or small MMU (Table 2.12). When the large MMU was used, the dominant edge type both numerically and proportionally (~50 % of the total number and length of those considered) was colonized pavement/continuous seagrass. In

contrast, when the small MMU was used, the number and length of that edge type was much reduced. Instead, use of the smaller MMU resulted in colonized pavement/sand edges becoming much more abundant in number and total length as well as a notable increase in the number of colonized pavement/patch reef (s) edges. Mean lengths of all edge types based on maps with large MMU were significantly longer than most edge types based on maps with small MMU (Table 2.12).

Discussion

Both spatial and thematic resolution of coral ecosystem maps heavily influenced the value of almost all landscape metrics derived from them. This indicates that the characterization of many of the typical components of coral ecosystems differed according to the thematic and spatial scales used in the study. Even the most general summary metrics comparing all four map conditions demonstrate major differences among maps. This study is the first analysis of the influence of spatial and thematic resolution of benthic cover maps; a topic that has been investigated previously only using neutral models and terrestrial systems. In general, the findings of this study are in agreement with those done previously. Rare map types became more common and dominant ones became less dominant when spatial resolution was increased (Turner et al. 1989, Benson and MacKenzie 1995, Stohlgren et al. 1997, Saura 2002, Lioubimtseva 2003). Small, simple polygons became more common in the map with smaller MMU (Saura 2002). Narrow polygons, highly patchy features, and those with one or more dimensions near the MMU were particularly sensitive to detection as spatial resolution decreased

(Andréfouët et al. 2003). This general agreement with prior work occurred despite this study's novel focus on benthic ecosystems (rather than neutral models or terrestrial systems) and methodological differences with prior work such as use of separately produced maps of different scales (rather than resampling of a high resolution map) and use of the distribution of individual polygon values in statistical comparisons (rather than average values for the entire map).

Characteristics of benthic maps of the Buck Island area differed depending on both the spatial and thematic resolution with which they were created. Increasing thematic resolution greatly increased the number of polygons, total edge length, and diversity of maps by splitting the space into more categories. Changing the MMU resulted in disproportionate changes by bottom type in nearly all metrics considered. For metrics generated based on whole maps, the range of values observed in number of polygons, average feature size, and total perimeter varied by an order of magnitude among maps. The direction, but not the magnitude of these changes could have been anticipated. Considering only these simplest of metrics it is clear that landscape ecological studies based on these aspects of the maps would have very different results depending on the thematic and spatial characteristics of the map used.

Which reef features are responsible for these changes and how do they influence landscape metrics at different spatial and thematic resolution? For maps with low thematic resolution, all three bottom types, hard bottom, submerged vegetation, and unconsolidated sediment were sensitive to MMU in at least one of the landscape metrics tested. Hard bottom showed the greatest sensitivity, with significantly different representation due to MMU in all four types of landscape

metrics evaluated. In fact, all four landscape metrics representing hard bottom polygons mapped with small MMU were significantly lower than nearly all other bottom types and MMU combinations. This indicates that many small, simple, and closely spaced hard bottom shapes became apparent when the smaller MMU was adopted. Indeed, visual inspection of the maps confirms the presence of many small, round patches of hard bottom mapped with the smaller MMU. Unconsolidated sediment and submerged vegetation were slightly less sensitive to MMU showing significant ($p < 0.05$) or nearly significant ($p \leq 0.07$) differences in three of the four families of landscape metrics that were considered. More specifically, the small MMU map exhibited a disproportionately large increase in the number of small unconsolidated sediment polygons relative to maps with larger MMU. There was also a major increase in the total perimeter of unconsolidated sediment polygons but only a relatively small increase in their total area for the map with the small MMU. This means that the small unconsolidated sediment polygons that were added must have been long, narrow polygons. This is supported by mean shape index values which were high for unconsolidated sediment whether produced using the large or small MMU. Again, visual inspection of the maps confirms that when the small MMU was used, many long narrow unconsolidated sediment polygons were added such as unconsolidated sediment channels or grooves in hard bottom and unconsolidated sediment halos between hard bottom and submerged vegetation.

The patterns described above can be further elucidated by considering the results of the edge analyses. When the MMU was reduced, the number of edges of all types increased most dramatically for unconsolidated sediment/hard bottom edges

(from 23 to 634). This means that many new edges between hard bottom and unconsolidated sediment were created by using the smaller MMU. Unconsolidated sediment halos around small patches of hard bottom and unconsolidated sediment channels in hard bottom both meet this criterion. Indeed, the edge length between unconsolidated sediment/hard bottom polygons was quite long when mapped with larger MMU yet significantly shorter than all other types when mapped with small MMU. These patterns and the specific features of the reef ecosystem responsible for them are made even clearer when the results from high thematic resolution maps are considered.

In comparisons between maps with high thematic resolution, the small MMU map had substantially higher numbers and total edge length of sand polygons. This indicated that many long, narrow sand polygons were added. Indeed, by using the smaller MMU and high thematic resolution, many sand halos around patch reefs and colonized pavement were added. These observations are supported by a large increase in number of colonized pavement / sand and patch reef (s) / sand edges when smaller MMU was used. Sand halos 5 to 10 meters wide separating reef and seagrass meadows are formed by grazing activities of herbivorous fish and invertebrates that rely on hard bottom as a structural refuge and only venture away a certain distance to feed on adjacent seagrass meadows (Randall 1965, Ogden et al. 1973). Similar to halos, long sand channels in pavement were also resolved only in maps with small MMU and contributed to the large increase in number and total edge length of sand polygons as well as the number of colonized pavement/sand edges. The spur and groove formations, common features of many reefs worldwide, are low relief in the

study area and are more appropriately described as colonized pavement with sand channels since the ‘spur and groove’ terminology typically connotes features with higher relief coral or spur components. The colonized pavement in the study area is quit flat and expansive and lies along much of the northern edge of the Buck Island bank. Well-developed sand channels occur in many parts of the pavement. The sand channels are typically 20 to 30 meters apart, 5 to 10 meters wide, and 50 to 300 m long although spacing, width, and length show considerable variability.

Small, simple patches became much more abundant in the map with smaller MMU, an observation that is consistent with prior studies (Saura 2002). Specifically, there was a very large increase in the number of patch reef polygons when the smaller MMU was used. Despite this increase, the total edge length of patch reef increased only modestly and the total area of patch reef actually declined. The per-polygon results from the Monte Carlo resampling analysis indicated that by using the small MMU, the patch reefs that were added were quite small in area and perimeter and formed very simple shapes. This makes sense since patch reefs are often small and circular. The area responsible for this appears to be the large number of patch reefs located northeast of the Buck Island lagoon. These features lie in ~10m water, extend nearly to the surface, are separated from each other and surrounded by a colonized pavement bottom, have a roughly circular footprint with a diameter of ~15 to 25 m, and were only mapped individually using the small MMU. This pattern is further quantified by the large increase in number of colonized pavement / patch reef (s) edges and the significant reduction in their mean length when smaller MMU was used.

As expected, MSI was lower when smaller MMU was used which indicates that overall, the area was characterized using many additional small shapes with low complexity relative to maps with large MMU (Saura 2002). Also of note, regardless of MMU, shape index was generally lowest for hard bottom and highest for unconsolidated sediment. This indicates that most hard bottom polygons were simpler in shape whereas soft bottom had longer or more complex edges. This makes sense considering the some of the common hard versus soft bottom features of coral reef ecosystems discussed so far such as patch reefs, which are typically round, and sand channels or halos which are typically long and narrow.

The results highlighted thus far indicate that some bottom features such as sand channels, halo's, and patch reef (s) occurred with dimensions intermediate between the two spatial scales examined in this study and consequently experienced very different characterization by landscape parameters depending on the spatial and thematic resolution of maps. A similar sensitivity to some landscape properties of coral atolls, such as rim aperture has been found when comparing atolls mapped with satellite data through a range of spatial resolutions (Andréfouët et al. 2003). Landscape properties changed dramatically when typical feature dimensions began to approach the spatial resolution of the satellite data. The extreme case of this occurs when sensor resolution is equal to or greater than feature size and features cannot be detected at all. In contrast to patch reefs and sand in the present study, linear reefs and continuous seagrass areas exhibited little change in any landscape metric evaluated (the only exception being NN for continuous seagrass). This is due to the broad size and simple edge of these features. Unlike sand and patch reefs, landscape

metrics representing linear reefs and continuous seagrass are apparently insensitive to changes in MMU at the levels evaluated in this study. For some benthic features such as these, both spatial scales evaluated in this study lie within the same domain of scale for those features (Weins 1989), for others, such as sand and patch reefs the changing MMU resulted in a dramatically different characterization.

Patchy habitats such as both categories of patchy seagrass and scattered coral and rock in sand also experienced major changes in characterization depending on MMU. When small MMU was used, all three of these bottom types were represented by many additional, small, simple polygons although total area declined. Inspection of these areas in the maps reveals that the heterogeneities of these patchy bottom types were lumped together when large MMU was used but were able to be separated out into smaller components with the smaller MMU. In many cases, small sand areas were able to be mapped within and between scattered coral and seagrass patches which further contributed to the large increase in number, perimeter, and total area of sand polygons discussed above. This was especially apparent for very patchy seagrass (10-50%) which was one of the very few bottom types to lose perimeter and a large proportion of its total area when smaller MMU was used.

The perception of landscape connectivity also changed dramatically depending on the thematic and spatial resolution used to create maps (Stohlgren et al. 1997). Overall, nearest neighbor (NN) values were shorter when the small MMU was used. Naturally, individual fish respond to and interact with connections within the actual landscape, but one's perception and ability to properly model the landscape's connectivity based on an organisms home range and willingness to cross open space

for example is heavily influenced by the choice of thematic and spatial resolution during mapping. Results of a tagging study that evaluated the movement patterns of many common Caribbean reef fish within and among reefs indicated that sand areas greater than 20 m wide separating reefs act as an effective barrier to fish movement between reefs for many species (Chapman and Kramer 2000). Interestingly, in the present study when small MMU was used, nearly half (49%) of all hard bottom patches had a NN distance less than 20 m, whereas when large MMU was used, only 21% of hard bottom patches had neighbors within that distance. Clearly, use of maps with low thematic resolution from the present study would have a major influence on the perceived connectivity of individual hard bottom patches for those species reluctant to travel across >20 m wide sand or seagrass patches to nearby hard bottom. Less is known about movement patterns of fish among and across habitat patches from the more detailed classifications used in this study. Nevertheless, the perception of landscape connectivity for fish that specialize on patch reef occupancy for example, would be dramatically different given the much lower NN values for this bottom type when mapped with small vs. large MMU. Field studies have shown that patch reef isolation and size effect reef fish recruitment and microhabitat selection (Schroeder 1987, Nanami and Nishihira 2003). Extrapolation of the results of such studies to broader spatial scales using landscape maps would be sensitive to the connectivity and patch sizes represented in those maps.

When MMU was decreased and smaller features were mapped, the dominant bottom types became less dominant and the rare bottom types became more common. This pattern was consistent for both thematic resolutions evaluated in the present

study. In the comparison of maps with only a few classifications it was observed that when MMU size was smaller, unconsolidated sediment, a rare bottom type, increased in area whereas hard bottom, the dominant bottom type, decreased in area. Similarly, in the comparison of maps with more classifications it was observed that four rare bottom types, absent in maps with large MMU, appeared in benthic maps only when the small MMU was used. Studies using neutral models and terrestrial landscapes have shown this same pattern. Reducing the MMU allows smaller, rare landscape features to be mapped separately from the larger features that they are adjacent to or encompassed by (Turner et al. 1989, Benson and MacKenzie 1995, Saura 2002).

These findings have important implications for the recent trend towards ecosystem based management of coral reefs and associated benthic habitats. The calls for protection of a certain percentage of shelf area (USCRTF 2000) or area of a certain habitat type such as “coral reefs” are dependent upon benthic maps for implementation. The results presented here indicate that if the goal were to protect, for example, 20% of the reef, the location and size of the area selected for protection may differ depending on the spatial and thematic characteristics of the benthic maps used in the selection process (Leslie et al. 2003). Once a site is selected, the belief is that 20% of the reef is protected based on a benthic map, but in reality, this is an abstraction of the actual amount of target habitat. Similarly, if 20% of the entire shelf was protected rather than targeting a specific bottom type, the perceived amounts and proportions of each bottom type in the managed area would differ depending on the characteristics of the map used (Leslie et al. 2003). For example, if the present study area were set aside as an MPA, the perceived total amount of hard bottom could differ

by as much as 12% (3185 ha when the large MMU is used relative to 2808 ha when the small MMU is used).

Too large an MMU means that potentially important but small patches are missed (Stohlgren et al. 1997). Rare habitats in this study area such as macroalgae for example, didn't appear in the benthic map until the smaller MMU was used during map production. Some macroalgae species have been identified as an important settlement and juvenile habitat for commercially significant species such as Nassau grouper, *Epinephelus striatus* (Dahlgren and Eggleston, 2001) and spiny lobster, *Panulirus argus* (Hernkind and Butler 1986). Choice of MMU changes our perception of the landscape as possessing a rare but key initial habitat for these species.

The results indicate that comparing properties among coral ecosystem areas or for a time series of a single area must be done cautiously if maps with differing spatial and thematic resolution are to be used. The present results and even those of some terrestrial studies, since general patterns were similar (Wu et al. 2002, Saura 2004, Urban 2005), could be used to provide correction factors for some scales to facilitate comparisons between areas mapped with differing parameters.

For maps with low thematic resolution, landscape diversity was higher when small MMU was used since area and number of polygons in each category achieved more equitable distributions. In contrast, our perception of landscape diversity at high thematic resolution experienced some unexpected changes when smaller MMU was used. Saura (2002) hypothesized that since more bottom types were mapped using smaller MMU, diversity would increase. However, my results indicated that

this effect was apparently not enough to overcome the highly inequitable distributions, especially in numbers of polygons, mapped at small MMU. This indicates that activities such as modeling species diversity based on landscape diversity or identifying MPA candidate sites to protect habitat diversity must carefully consider the characteristics of source maps. Diversity of coral ecosystem maps produced with different levels of spatial and thematic resolution can vary in unpredictable ways.

Differences found between maps compared in this study are due to their spatial and thematic characteristics, not to some difference in accuracy or production technique. Overall thematic accuracy was estimated to be 94% for the coarse thematic and spatial resolution map of the study area (Kendall et al. 2004). Fine-scale maps were produced using the identical imagery and approach coupled with much more extensive field surveys to accommodate the higher spatial detail. Fine-scale, thematically detailed benthic maps of coral ecosystems elsewhere have been shown to have similarly high levels of classification accuracy (e.g. NOAA/NCCOS 2005). Therefore, each map compared in this study is assumed to be an acceptable abstraction of the actual benthic features at this place given the scale and thematic classes with which it was created. Also, recall that some categories in the original maps with large MMU, specifically “colonized pavement with sand channels” and “aggregate patch reefs”, required modification to improve map comparability. The original intent behind the use of such categories was to at least thematically separate areas that exhibit heterogeneity at finer-scales than can be mapped in separate small polygons. That these categories were not able to be used in fine-scale maps was the

first indication that changing spatial scale results in different characterization of some bottom features.

A caveat in nearly all discussions of landscape analysis is that the results are heavily dependent on the particular location, range of scales considered, extent, and map classes used in the analyses. The specific findings of this study, based on a single landscape which possesses both typical and unique coral ecosystem components, must be cautiously applied to other benthic landscapes with different proportions of bottom types and reef morphologies. In addition, the present study examined only two levels of spatial and thematic resolution respectively. Prior studies using neutral models and land cover maps showed non-linear changes in some landscape metrics when examined through a wide range of grain sizes and thematic resolutions (Turner et al. 1989, Wu et al. 2002, Manson et al. 2003, Neel et al. 2004, Shen et al. 2004, Huang et al. 2006). For most metrics, results are only applicable within the range of values studied and for similar landscapes. Extrapolation significantly beyond those scales or in landscapes with quite different spatial properties is often inappropriate (Wiens 1989, Wickham and Riitters 1995, Qi and Wu 1996, Wu et al. 2002, Neel et al. 2004).

Individual organisms sense and respond to landscape cues through a variety of mechanisms, but scientists and managers can only perceive an organism's regional landscape through the limited lens of remote sensing and benthic maps (Milne 1992). Several recent studies have used coral ecosystem maps to predict broad scale fish distributions by identifying correlations between the distribution of fishes and their local (Christensen et al. 2003, Kendall et al. 2003) or surrounding landscape (Kendall

et al. 2003, Kendall 2005). For example, diversity of fish on reefs has been correlated with amount of seagrass surrounding them (Kendall 2005) and distribution of juvenile French grunts, *Haemulon flavolineatum*, is related to the relative proximities of hard and soft bottom habitat (Kendall et al. 2003). The results of the present study indicate that such findings may have been different had maps with smaller or larger MMU or different thematic resolution been used. Conducting such studies using maps with different spatial and thematic resolution and comparing the results is the focus of subsequent chapters.

This study indicates that most features of the reef ecosystem are sensitive to changes in thematic and spatial resolution of the maps characterizing them. Hard bottom in general, especially the patch reef and colonized pavement components, as well as sand areas and patchy features were among the most sensitive to change in spatial resolution. In contrast, linear reef and relatively continuous seagrass features were quite consistently characterized regardless of MMU. The data demonstrated that the properties of coral ecosystem maps must be considered and understood for their successful application in science and management. Too large an MMU or too coarse a classification scheme may suggest the presence of large areas of homogenous habitat when in reality none exist (Stohlgren et al. 1997). Too small an MMU may be unnecessarily detailed, expensive, or time consuming to meet the objectives of a given project. If properties of landscape maps are not well understood, there is great potential for drawing erroneous conclusions in applications in which they are used as a basic information input (Saura 2002).

Table 2.1: Hierarchically structured list of bottom types in the benthic maps. Cells at right indicate the sensitivity of each thematic category to being mapped at different MMUs according to four commonly used landscape metrics (SI= shape index, NN=nearest neighbor index). Cells contain p-values from resampling statistics. Blank cells denote bottom types not evaluated in this comparison since one or both of the pair (2 MMUs) did not have sufficient sample size. Those within grey cells denote a significant difference found in the Monte Carlo resampling test at the <0.05 level for a given landscape metric and bottom type when mapped with small versus large MMU. A bold p-value denotes a comparison that was significantly different when the non-parametric Dunn's test was used.

Main thematic categories Nested thematic subcategories	Landscape metric			
	Area	Peri- meter	SI	NN
Unconsolidated Sediments (0-10 % submerged vegetation)	0.06	0.07	0.42	0.03
Mud				
Sand	0.06	0.06	0.47	<0.01
Submerged Vegetation	<0.01	0.09	0.04	0.07
Continuous Macroalgae (90- 100 % cover)				
Patchy Macroalgae (50-90 % cover)				
Patchy Macroalgae (10-50 % cover)				
Continuous Seagrass (90- 100 % cover)	0.13	0.22	0.16	<0.01
Patchy Seagrass (50-90 % cover)	0.01	<0.01	<0.01	<0.01
Patchy Seagrass (10-50 % cover)	<0.01	<0.01	<0.01	0.02
Hard Bottom	<0.01	0.02	<0.01	0.02
Colonized Bedrock				
Colonized Pavement	0.02	0.14	<0.01	<0.01
Linear Reef	0.29	0.33	0.38	0.31
Patch Reef (s)	<0.01	<0.01	<0.01	<0.01
Reef Rubble				
Scattered Coral/Rock in Sand	<0.01	0.01	0.01	<0.01
Other Delineations				
Artificial				
Land				
Mangrove				

Table 2.2: Summary metrics based on whole maps. See text for definition of metrics.

	Large MMU Few Categories	Large MMU Many Categories	Small MMU Few Categories	Small MMU Many Categories
Number of polygons:	113	311	1069	2497
Avg. polygon area (ha):	51.4	18.7	5.4	2.3
Sum of edges (km)	225	423	465	790
1/Simpson Diversity (#, area):	2.04, 1.98	6.62, 3.94	2.42, 2.39	5.42, 3.90
Shannon Diversity (#, area):	0.37, 0.35	0.90, 0.76	0.42, 0.42	0.85, 0.75
Mean Shape Index:	1.7	1.9	1.5	1.4
Mean Nearest-Neighbor (m):	131	152	44	55

Table 2.3: Matrix of the influence of MMU size and bottom type on **area** for polygons mapped using low thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	1 acre Submerged Vegetation	1 acre Hard Bottom	1 acre Unconsolidated Sediment	100 m ² Submerged Vegetation	100 m ² Hard Bottom	100 m ² Unconsolidated Sediment	Mean (ha)
1 acre Submerged Vegetation	0.52	0.18	0.00	0.00	0.03	0.00	96.5
1 acre Hard Bottom		0.50	0.00	0.00	0.00	0.00	43.6
1 acre Unconsolidated Sediment			0.51	0.11	0.07	0.06	13.2
100 m ² Submerged Vegetation				0.51	0.22	0.00	8.7
100 m ² Hard Bottom					0.50	0.02	4.8
100 m ² Unconsolidated Sediment						0.50	2.6

Table 2.4: Matrix of the influence of MMU size and bottom type on **perimeter** for polygons mapped using low thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	1 acre Submerged Vegetation	1 acre Unconsolidated Sediment	1 acre Hard Bottom	100 m ² Submerged Vegetation	100 m ² Unconsolidated Sediment	100 m ² Hard Bottom	Mean (m)
1 acre Submerged Vegetation	0.49	0.00	0.03	0.09	0.00	0.00	9257
1 acre Unconsolidated Sediment		0.49	0.24	0.11	0.07	0.04	2684
1 acre Hard Bottom			0.50	0.32	0.03	0.02	2449
100 m ² Submerged Vegetation				0.50	0.14	0.02	1510
100 m ² Unconsolidated Sediment					0.50	0.08	1003
100 m ² Hard Bottom						0.50	515

Table 2.5: Matrix of the influence of MMU size and bottom type on **shape index** for polygons mapped using low thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	100 m ² Unconsolidated Sediment	1 acre Submerged Vegetation	1 acre Unconsolidated Sediment	1 acre Hard Bottom	100 m ² Submerged Vegetation	100 m ² Hard Bottom	Mean
100 m ² Unconsolidated Sediment	0.50	0.51	0.42	0.00	0.00	0.00	2.163
1 acre Submerged Vegetation		0.49	0.42	0.02	0.04	0.00	2.136
1 acre Unconsolidated Sediment			0.50	0.01	0.02	0.00	2.089
1 acre Hard Bottom				0.49	0.38	0.00	1.492
100 m ² Submerged Vegetation					0.50	0.00	1.454
100 m ² Hard Bottom						0.50	1.083

Table 2.6: Matrix of the influence of MMU size and bottom type on **nearest neighbor** for polygons mapped using low thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	100 m ² Unconsolidated Sediment	1 acre Submerged Vegetation	1 acre Unconsolidated Sediment	1 acre Hard Bottom	100 m ² Submerged Vegetation	100 m ² Hard Bottom	Mean (m)
100 m ² Unconsolidated Sediment	0.49	0.00	0.03	0.09	0.00	0.00	227
1 acre Submerged Vegetation		0.49	0.24	0.11	0.07	0.04	80
1 acre Unconsolidated Sediment			0.50	0.32	0.03	0.02	58
1 acre Hard Bottom				0.50	0.14	0.02	43
100 m ² Submerged Vegetation					0.50	0.08	37
100 m ² Hard Bottom						0.50	33

Table 2.7: Matrix of the influence of MMU size and bottom type on **edge length** for polygons mapped using low thematic resolution. Each edge type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	1 acre Unconsolidated Sed. / Sub. Veg.	1 acre Submerged Vegetation / Hard Bottom	1 acre Unconsolidated Sed. / Hard Bottom	100 m ² Submerged Vegetation / Hard Bottom	100 m ² Unconsolidated Sed. / Sub. Veg.	100 m ² Unconsolidated Sed. / Hard Bottom	Mean (m)	n	total (km)
1 acre Unconsolidated Sed. / Sub. Veg.	0.50	0.38	0.15	0.00	0.00	0.00	1481	16	24
1 acre Submerged Vegetation / Hard Bottom		0.50	0.30	0.00	0.00	0.00	1341	90	121
1 acre Unconsolidated Sed. / Hard Bottom			0.50	0.00	0.00	0.00	1054	23	24
100 m ² Submerged Vegetation / Hard Bottom				0.51	0.29	0.00	430	251	108
100 m ² Unconsolidated Sed. / Sub. Veg.					0.49	0.00	391	332	130
100 m ² Unconsolidated Sed. / Hard Bottom						0.50	263	634	167

Table 2.8: Matrix of the influence of MMU size and bottom type on **area** for polygons mapped using high thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	1 acre Continuous Seagrass	1 acre Colonized Pavement	1 acre Patch Reef (s)	1 acre Sand	100 m ² Continuous Seagrass	1 acre 10 - 50% Patchy Seagrass	1 acre Linear Reef	1 acre 50 - 90% Patchy Seagrass	1 acre Scattered Coral and Rock in Sand	100 m ² Linear Reef	100 m ² Colonized Pavement	100 m ² Sand	100 m ² Reef Rubble	100 m ² 50 - 90% Patchy Seagrass	100 m ² 10 - 50% Patchy Macroalgae	100 m ² Colonized Bedrock	100 m ² Scattered Coral and Rock in Sand	100 m ² 10 - 50% Patchy Seagrass	100 m ² Patch Reef (s)	100 m ² Artificial	Mean (m ²)
1 acre Continuous Seagrass	0.48	0.30	0.37	0.35	0.13	0.18	0.28	0.14	0.12	0.15	0.05	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	291506
1 acre Colonized Pavement		0.49	0.66	0.62	0.31	0.42	0.58	0.36	0.29	0.29	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	252365
1 acre Patch Reef (s)			0.50	0.46	0.22	0.30	0.01	0.16	0.29	0.00	0.03	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	169988
1 acre Sand				0.49	0.28	0.37	0.34	0.23	0.28	0.19	0.04	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	137179
100 m ² Continuous Seagrass					0.51	0.44	0.48	0.30	0.26	0.07	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	117316
1 acre 10 - 50% Patchy Seagrass						0.50	0.55	0.36	0.37	0.37	0.07	0.08	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	105392
1 acre Linear Reef							0.50	0.38	0.34	0.29	0.08	0.11	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	96518
1 acre 50 - 90% Patchy Seagrass								0.51	0.51	0.50	0.07	0.10	0.11	0.01	0.00	0.00	0.00	0.00	0.00	0.00	85020
1 acre Scattered Coral and Rock in Sand									0.50	0.57	0.09	0.13	0.15	0.01	0.00	0.00	0.00	0.00	0.00	0.00	82859
100 m ² Linear Reef										0.51	0.12	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	68137
100 m ² Colonized Pavement											0.50	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	39761
100 m ² Sand												0.49	0.84	0.41	0.61	0.68	0.16	0.18	0.00	0.00	25545
100 m ² Reef Rubble													0.51	0.18	0.14	0.09	0.09	0.00	0.00	0.00	23689
100 m ² 50 - 90% Patchy Seagrass														0.50	0.40	0.48	0.07	0.00	0.00	0.00	16939
100 m ² 10 - 50% Patchy Macroalgae															0.49	0.55	0.21	0.02	0.00	0.00	13907
100 m ² Colonized Bedrock																0.50	0.17	0.02	0.00	0.00	13756
100 m ² Scattered Coral and Rock in Sand																	0.50	0.41	0.00	0.00	9199
100 m ² 10 - 50% Patchy Seagrass																		0.50	0.00	0.00	6963
100 m ² Patch Reef (s)																			0.50	0.45	1241
100 m ² Artificial																				0.51	799

Table 2.9: Matrix of the influence of MMU size and bottom type on **perimeter** for polygons mapped using high thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	1 acre Continuous Seagrass	1 acre 10 - 50% Patchy Seagrass	1 acre Sand	100 m ² Continuous Seagrass	1 acre Linear Reef	1 acre 50 - 90% Patchy Seagrass	1 acre Patch Reef (s)	1 acre Colonized Pavement	100 m ² Linear Reef	1 acre Scattered Coral and Rock in Sand	100 m ² Reef Rubble	100 m ² Colonized Bedrock	100 m ² Sand	100 m ² 50 - 90% Patchy Seagrass	100 m ² 10 - 50% Patchy Macroalgae	100 m ² Colonized Pavement	100 m ² Scattered Coral and Rock in Sand	100 m ² 10 - 50% Patchy Seagrass	100 m ² Artificial	100 m ² Patch Reef (s)	Mean (m)
1 acre Continuous Seagrass	0.50	0.23	0.33	0.22	0.30	0.17	0.24	0.08	0.20	0.10	0.06	0.04	0.01	0.00	0.00	0.05	0.00	0.00	0.00	0.00	4924
1 acre 10 - 50% Patchy Seagrass		0.50	0.57	0.40	0.51	0.37	0.41	0.28	0.39	0.25	0.09	0.07	0.08	0.00	0.00	0.06	0.00	0.00	0.00	0.00	2745
1 acre Sand			0.50	0.30	0.39	0.33	0.32	0.21	0.21	0.18	0.01	0.01	0.06	0.00	0.00	0.04	0.01	0.00	0.00	0.00	2742
100 m ² Continuous Seagrass				0.50	0.51	0.34	0.42	0.25	0.28	0.16	0.00	0.00	0.01	0.00	0.00	0.13	0.00	0.00	0.00	0.00	2657
1 acre Linear Reef					0.50	0.41	0.41	0.25	0.33	0.27	0.02	0.03	0.08	0.00	0.00	0.03	0.05	0.00	0.00	0.00	2405
1 acre 50 - 90% Patchy Seagrass						0.50	0.46	0.38	0.47	0.36	0.12	0.09	0.11	0.00	0.00	0.06	0.01	0.00	0.00	0.00	2218
1 acre Patch Reef (s)							0.49	0.31	0.43	0.37	0.00	0.00	0.09	0.00	0.00	0.03	0.06	0.00	0.00	0.00	2081
1 acre Colonized Pavement								0.51	0.66	0.55	0.18	0.14	0.08	0.00	0.00	0.14	0.00	0.00	0.00	0.00	2045
100 m ² Linear Reef									0.51	0.41	0.04	0.04	0.10	0.00	0.00	0.04	0.05	0.00	0.00	0.00	2009
1 acre Scattered Coral and Rock in Sand										0.50	0.13	0.11	0.13	0.00	0.00	0.07	0.01	0.00	0.00	0.00	1890
100 m ² Reef Rubble											0.51	0.47	0.21	0.08	0.08	0.08	0.09	0.00	0.00	0.00	1088
100 m ² Colonized Bedrock												0.50	0.23	0.07	0.08	0.07	0.10	0.00	0.00	0.00	1087
100 m ² Sand													0.50	0.30	0.39	0.34	0.12	0.04	0.03	0.00	999
100 m ² 50 - 90% Patchy Seagrass														0.49	0.42	0.24	0.31	0.01	0.00	0.00	713
100 m ² 10 - 50% Patchy Macroalgae															0.50	0.14	0.26	0.07	0.02	0.00	676
100 m ² Colonized Pavement																0.50	0.33	0.00	0.00	0.00	673
100 m ² Scattered Coral and Rock in Sand																	0.51	0.37	0.16	0.00	602
100 m ² 10 - 50% Patchy Seagrass																		0.50	0.02	0.00	486
100 m ² Artificial																			0.49	0.03	260
100 m ² Patch Reef (s)																				0.50	116

Table 2.10: Matrix of the influence of MMU size and bottom type on **shape index** for polygons mapped using high thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	100 m ² Sand	1 acre Sand	100 m ² Colonized Bedrock	1 acre 10 - 50% Patchy Seagrass	1 acre Scattered Coral and Rock in Sand	1 acre Continuous Seagrass	1 acre 50 - 90% Patchy Seagrass	100 m ² Artificial	1 acre Linear Reef	100 m ² Reef Rubble	100 m ² Linear Reef	100 m ² Continuous Seagrass	1 acre Patch Reef (s)	100 m ² Scattered Coral and Rock in Sand	100 m ² 50 - 90% Patchy Seagrass	100 m ² 10 - 50% Patchy Macroalgae	1 acre Colonized Pavement	100 m ² 10 - 50% Patchy Seagrass	100 m ² Colonized Pavement	100 m ² Patch Reef (s)	Mean
100 m ² Sand	0.50	0.47	0.43	0.31	0.25	0.27	0.23	0.30	0.16	0.08	0.05	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.160
1 acre Sand		0.51	0.49	0.41	0.36	0.38	0.33	0.38	0.21	0.12	0.17	0.13	0.04	0.04	0.00	0.00	0.00	0.00	0.00	0.00	2.102
100 m ² Colonized Bedrock			0.49	0.44	0.39	0.40	0.36	0.39	0.27	0.20	0.19	0.10	0.08	0.02	0.00	0.00	0.00	0.00	0.00	0.00	2.099
1 acre 10 - 50% Patchy Seagrass				0.51	0.50	0.46	0.44	0.45	0.31	0.22	0.20	0.10	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.00	2.047
1 acre Scattered Coral and Rock in Sand					0.51	0.47	0.45	0.46	0.24	0.15	0.15	0.08	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	2.030
1 acre Continuous Seagrass						0.50	0.49	0.49	0.40	0.37	0.31	0.16	0.20	0.04	0.01	0.02	0.01	0.01	0.00	0.00	2.005
1 acre 50 - 90% Patchy Seagrass							0.50	0.49	0.32	0.23	0.24	0.12	0.08	0.03	0.00	0.00	0.00	0.00	0.00	0.00	2.002
100 m ² Artificial								0.49	0.39	0.37	0.34	0.22	0.26	0.09	0.03	0.05	0.04	0.03	0.00	0.00	1.973
1 acre Linear Reef									0.51	0.42	0.38	0.26	0.19	0.13	0.04	0.04	0.03	0.03	0.00	0.00	1.876
100 m ² Reef Rubble										0.49	0.46	0.27	0.19	0.15	0.04	0.05	0.03	0.03	0.00	0.00	1.833
100 m ² Linear Reef											0.50	0.33	0.32	0.18	0.06	0.08	0.05	0.04	0.00	0.00	1.809
100 m ² Continuous Seagrass												0.50	0.51	0.31	0.12	0.14	0.09	0.05	0.00	0.00	1.690
1 acre Patch Reef (s)													0.48	0.38	0.24	0.23	0.19	0.15	0.02	0.00	1.668
100 m ² Scattered Coral and Rock in Sand														0.50	0.21	0.22	0.13	0.06	0.00	0.00	1.637
100 m ² 50 - 90% Patchy Seagrass															0.51	0.38	0.26	0.17	0.00	0.00	1.573
100 m ² 10 - 50% Patchy Macroalgae																0.50	0.41	0.33	0.00	0.00	1.546
1 acre Colonized Pavement																	0.52	0.42	0.00	0.00	1.523
100 m ² 10 - 50% Patchy Seagrass																		0.51	0.00	0.00	1.505
100 m ² Colonized Pavement																			0.50	0.00	1.132
100 m ² Patch Reef (s)																				0.51	1.006

Table 2.11: Matrix of the influence of MMU size and bottom type on **nearest neighbor** for polygons mapped using high thematic resolution. Each bottom type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	100 m ² Artificial	100 m ² Reef Rubble	1 acre Patch Reef (s)	1 acre Sand	1 acre Linear Reef	1 acre Scattered Coral and Rock in Sand	1 acre 50 - 90% Patchy Seagrass	100 m ² Linear Reef	1 acre 10 - 50% Patchy Seagrass	100 m ² Colonized Bedrock	1 acre Continuous Seagrass	100 m ² 10 - 50% Patchy Macroalgae	1 acre Colonized Pavement	100 m ² 10 - 50% Patchy Seagrass	100 m ² 50 - 90% Patchy Seagrass	100 m ² Scattered Coral and Rock in Sand	100 m ² Continuous Seagrass	100 m ² Sand	100 m ² Colonized Pavement	100 m ² Patch Reef (s)	Mean (m)
100 m ² Artificial	0.50	0.45	0.32	0.12	0.08	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	397
100 m ² Reef Rubble		0.47	0.33	0.43	0.37	0.21	0.23	0.20	0.06	0.03	0.02	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	377
1 acre Patch Reef (s)			0.50	0.45	0.39	0.25	0.29	0.27	0.19	0.16	0.16	0.08	0.03	0.02	0.01	0.00	0.00	0.00	0.00	0.00	278
1 acre Sand				0.51	0.38	0.21	0.16	0.18	0.04	0.03	0.03	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	231
1 acre Linear Reef					0.51	0.40	0.32	0.31	0.11	0.08	0.08	0.12	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	194
1 acre Scattered Coral and Rock in Sand						0.50	0.42	0.30	0.10	0.07	0.05	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	176
1 acre 50 - 90% Patchy Seagrass							0.50	0.35	0.09	0.04	0.04	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	166
100 m ² Linear Reef								0.51	0.36	0.29	0.27	0.26	0.08	0.05	0.02	0.01	0.02	0.00	0.00	0.01	141
1 acre 10 - 50% Patchy Seagrass									0.49	0.30	0.28	0.33	0.05	0.02	0.00	0.00	0.00	0.00	0.00	0.00	121
100 m ² Colonized Bedrock										0.50	0.50	0.43	0.20	0.13	0.05	0.01	0.00	0.00	0.00	0.03	103
1 acre Continuous Seagrass											0.49	0.42	0.19	0.13	0.04	0.01	0.00	0.00	0.00	0.04	103
100 m ² 10 - 50% Patchy Macroalgae												0.50	0.34	0.26	0.13	0.03	0.08	0.01	0.00	0.00	100
1 acre Colonized Pavement													0.47	0.40	0.10	0.01	0.00	0.00	0.00	0.00	86
100 m ² 10 - 50% Patchy Seagrass														0.49	0.11	0.00	0.00	0.00	0.00	0.00	83
100 m ² 50 - 90% Patchy Seagrass															0.50	0.04	0.01	0.00	0.00	0.00	71
100 m ² Scattered Coral and Rock in Sand																0.50	0.25	0.03	0.00	0.00	56
100 m ² Continuous Seagrass																	0.50	0.24	0.01	0.10	49
100 m ² Sand																		0.51	0.01	0.00	43
100 m ² Colonized Pavement																			0.50	0.00	34
100 m ² Patch Reef (s)																				0.50	23

Table 2.12: Matrix of the influence of MMU size and bottom type on **length of edges** between polygons mapped using high thematic resolution. Each edge type and MMU combination are ordered from largest to smallest mean value (beginning in upper left corner). P-values in the matrix represent significance level of pairwise comparisons of the differences in means based on Monte Carlo resampling tests. Shaded cells denote differences that occurred by chance in less than 5% of the resampling runs.

	1 acre Colonized Pavement / Sand	1 acre Colonized Pavement / Patch Reef (s)	1 acre Colonized Pavement / Continuous Seagrass	100 m ² Colonized Pavement / Continuous Seagrass	100 m ² Linear Reef / Sand	100 m ² Colonized Pavement / Sand	1 acre Linear Reef / Continuous Seagrass	100 m ² Patch Reef (s) / Continuous Seagrass	100 m ² Colonized Pavement / Patch Reef (s)	100 m ² Patch Reef (s) / Sand	Mean (m)	n	total (km)
1 acre Colonized Pavement / Sand	0.53	0.44	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	847	23	19
1 acre Colonized Pavement / Patch Reef (s)		0.48	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	790	15	12
1 acre Colonized Pavement / Continuous Seagrass			0.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	666	65	43
100 m ² Colonized Pavement / Continuous Seagrass				0.50	0.25	0.08	0.20	0.00	0.00	0.00	307	55	17
100 m ² Linear Reef / Sand					0.50	0.23	0.44	0.00	0.00	0.00	259	59	15
100 m ² Colonized Pavement / Sand						0.50	0.59	0.00	0.00	0.00	221	496	109
1 acre Linear Reef / Continuous Seagrass							0.49	0.01	0.00	0.00	203	11	2
100 m ² Patch Reef (s) / Continuous Seagrass								0.49	0.36	0.31	91	23	2
100 m ² Colonized Pavement / Patch Reef (s)									0.50	0.29	88	514	45
100 m ² Patch Reef (s) / Sand										0.50	84	202	17

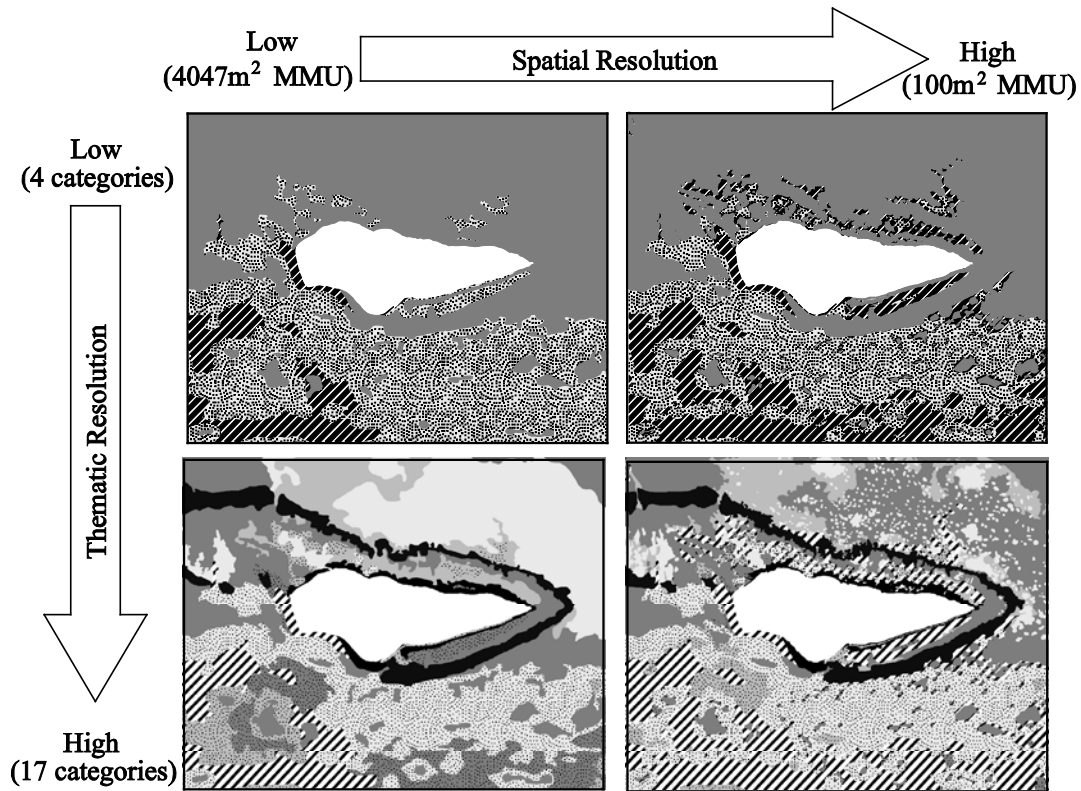


Figure 2.1: The four unique combinations of low and high spatial and thematic resolution of maps investigated in this study. The scale is zoomed in to a small subset of the entire study area immediately around Buck Island (center white) to convey the conceptual design of the study as well as the map detail at the corresponding levels of spatial and thematic resolution. Solid grays denote hard bottom and its subcategories, stippling denotes submerged vegetation and its subcategories, and slashing denotes unconsolidated sediments. All mapped categories are not shown in this extent.

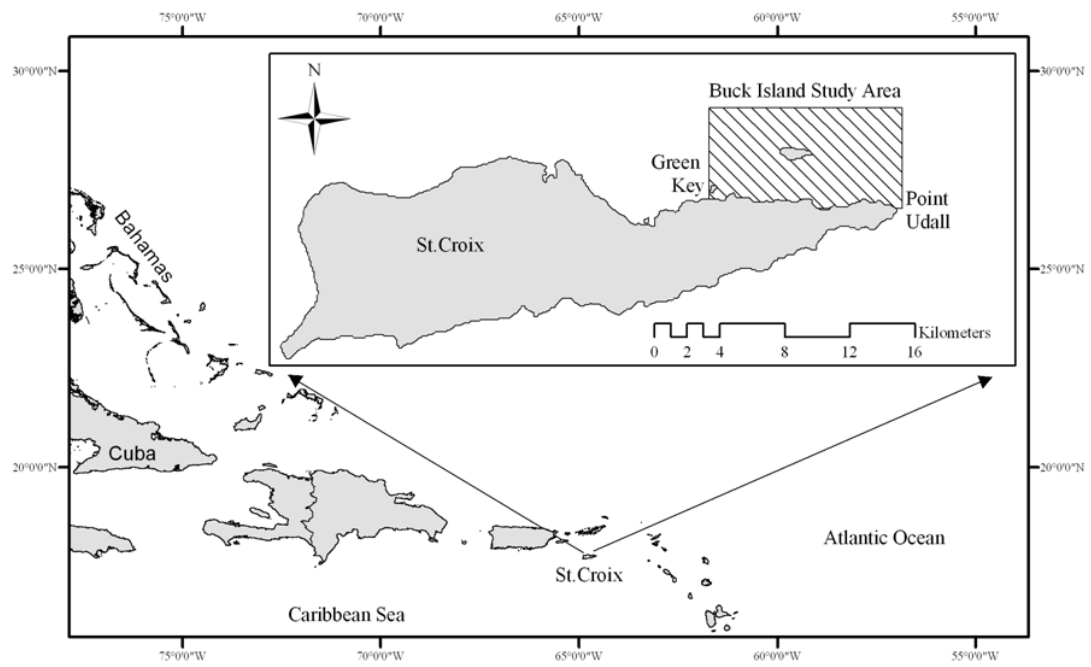


Figure 2.2: The study area around Buck Island, St. Croix.

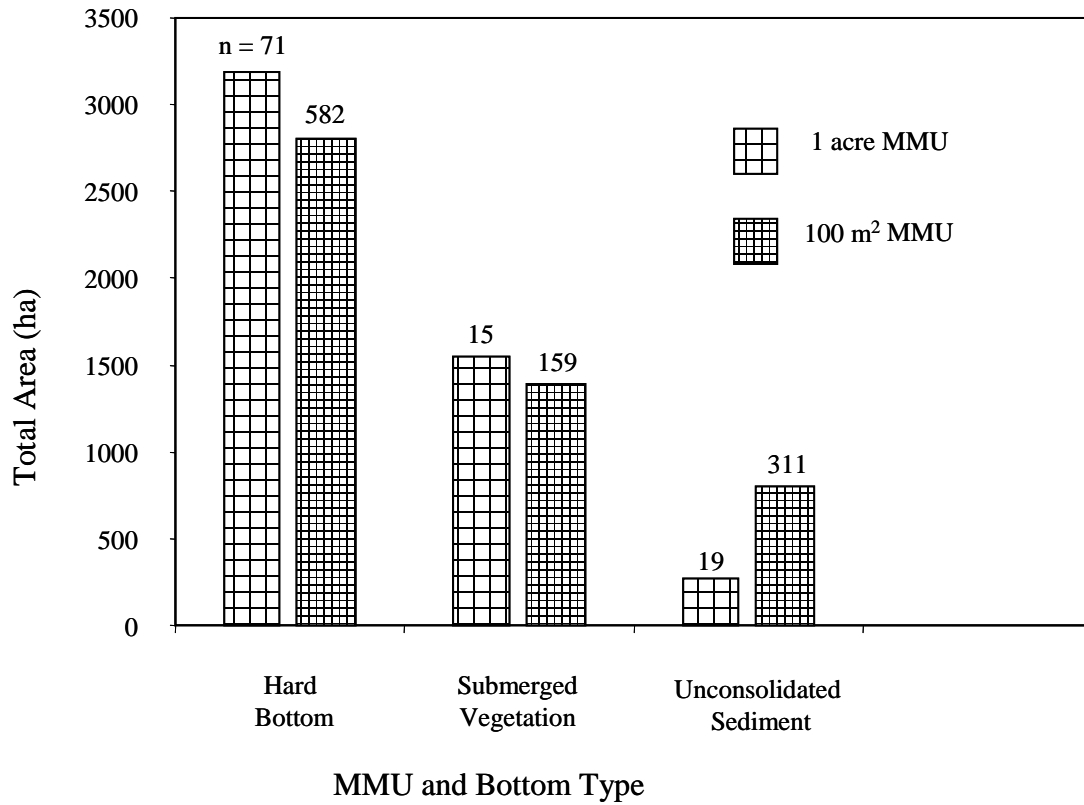


Figure 2.3: Influence of MMU size on the total area of each bottom type mapped using low thematic resolution. Number of polygons of each type is provided above each bar.

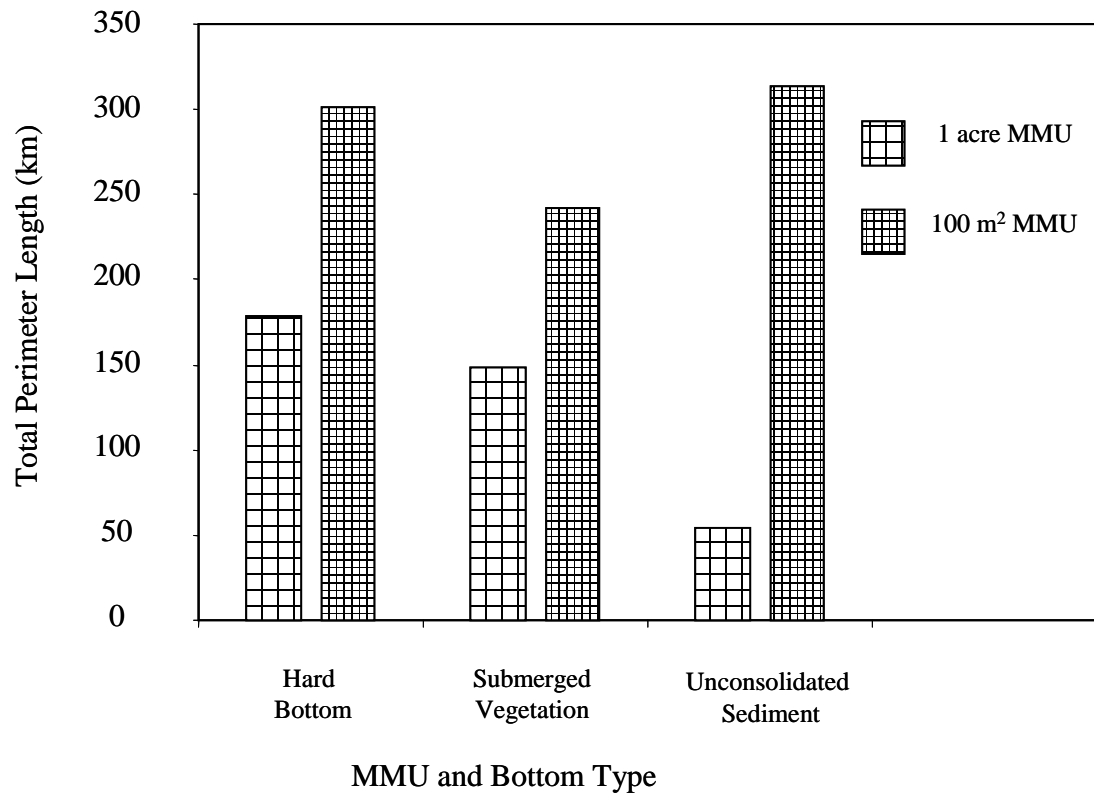


Figure 2.4: Influence of MMU size on the total perimeter of each bottom type mapped using low thematic resolution.

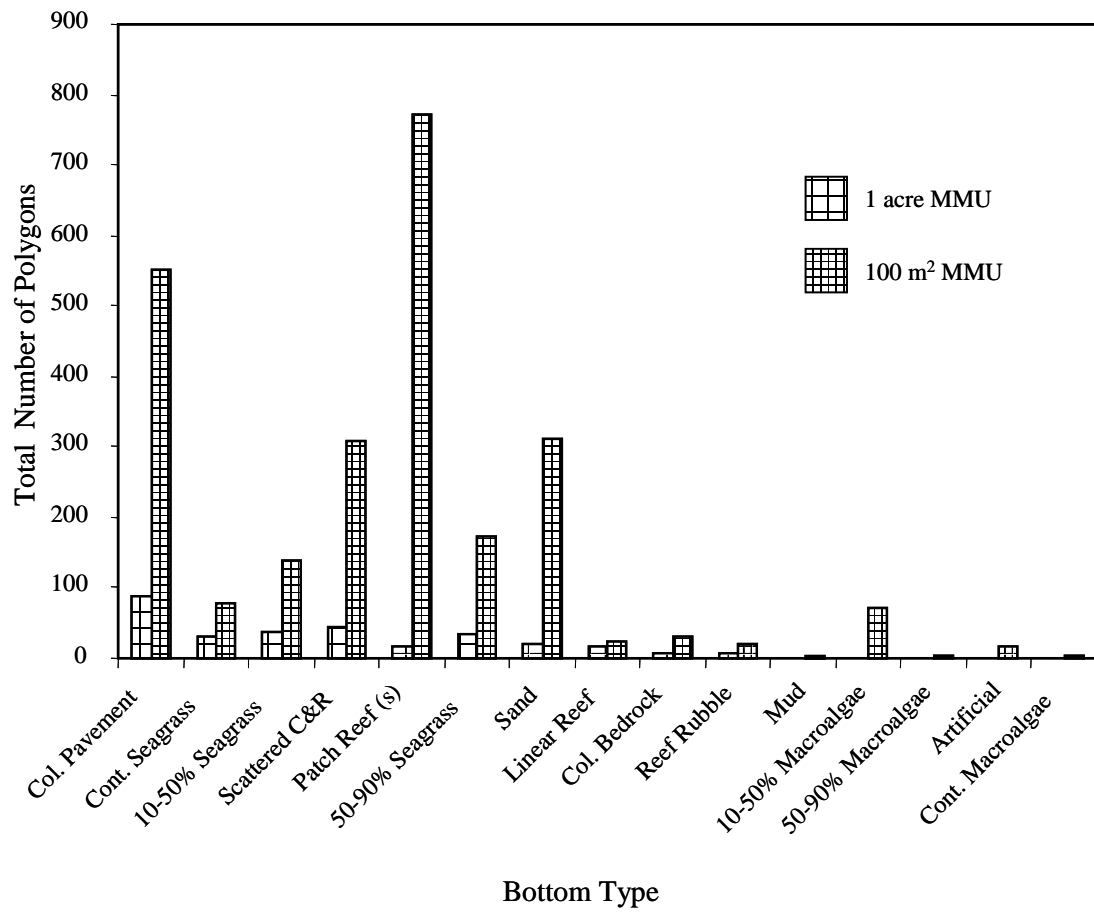


Figure 2.5: Total number of polygons mapped by bottom type and MMU using high thematic resolution.

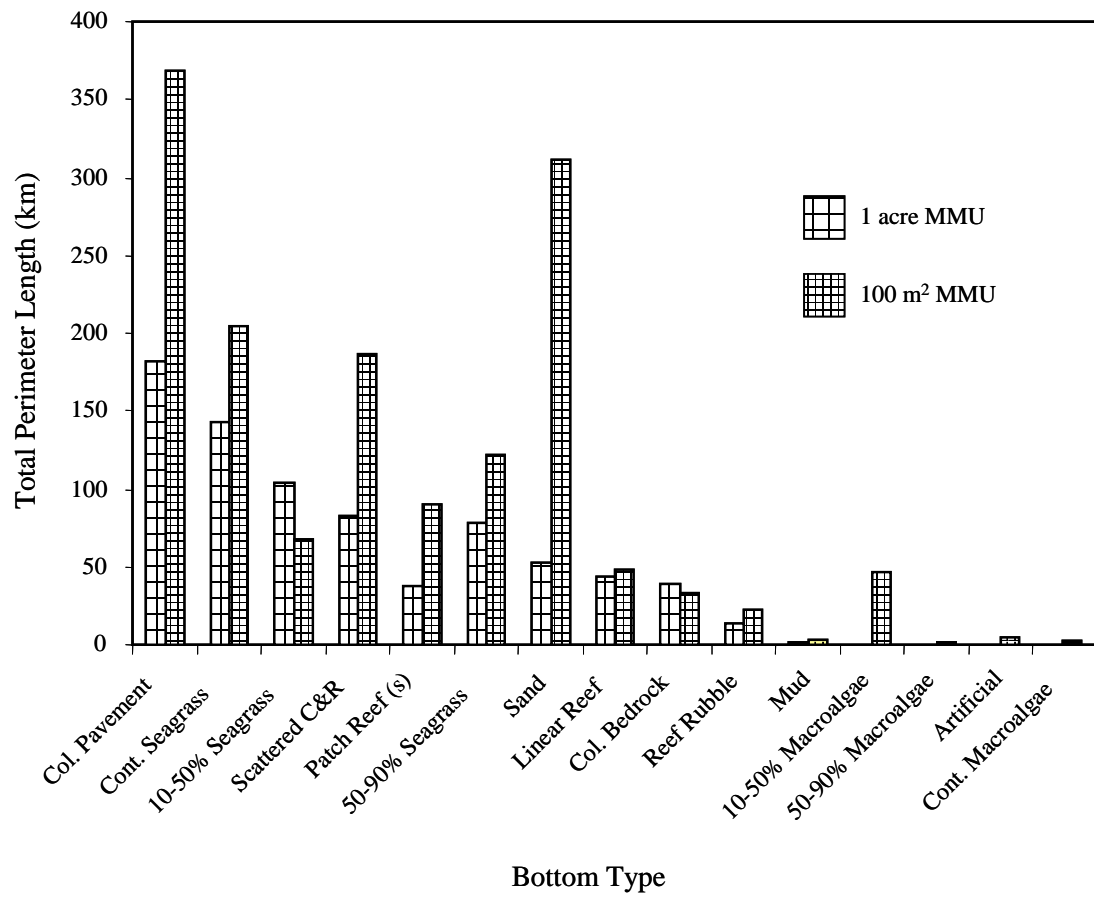


Figure 2.6: Total perimeter mapped by bottom type and MMU using high thematic resolution.

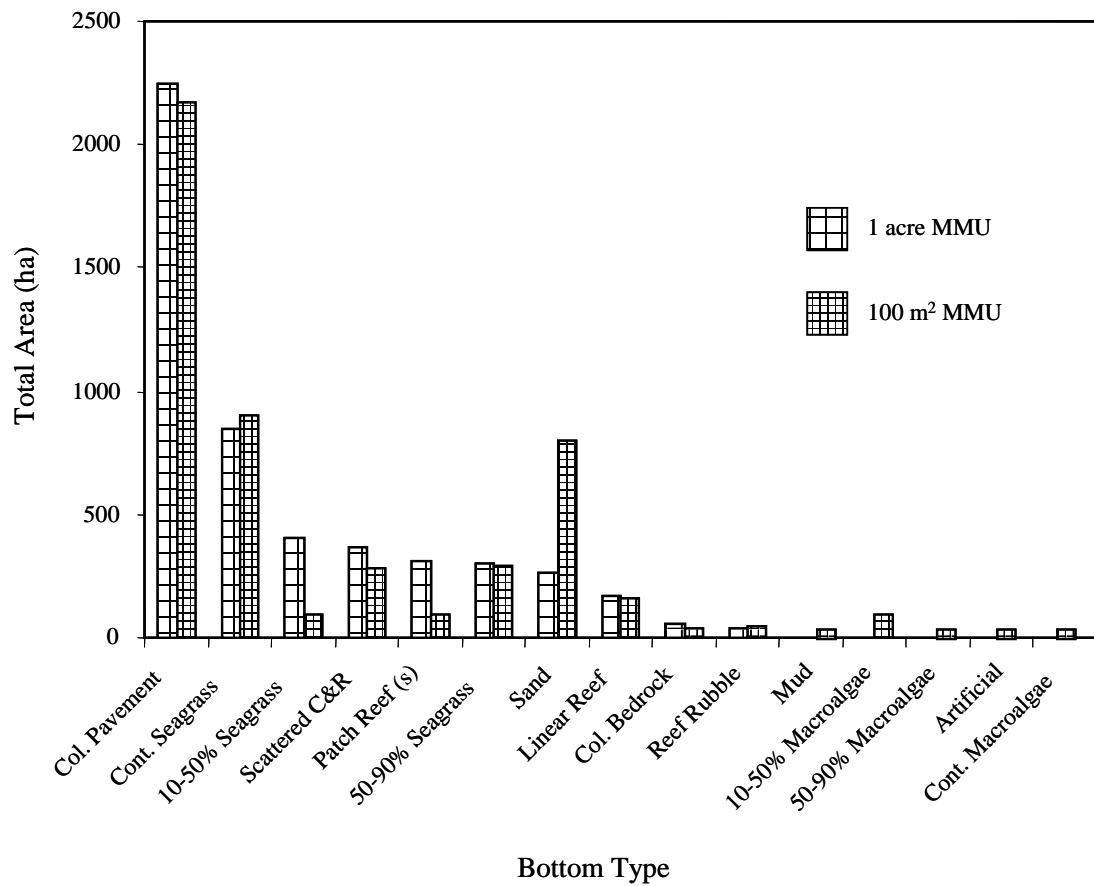


Figure 2.7: Total area mapped by bottom type and MMU using high thematic resolution.

Chapter 3: Relationships among fish assemblages, habitat variables, and benthic maps.

Abstract

Benthic maps are broad-scale characterizations that lack the detailed environmental attributes that have been the focus of most prior empirical studies linking reef fish and habitat. Here, I used multivariate analyses to quantify correlations among fish assemblages, local habitat variables, and the reef types that are depicted in benthic maps. Benthic maps of a study system in St. Croix, U.S. Virgin Islands with high (100 m² minimum mapping unit) and low (4048 m² minimum mapping unit) spatial resolution respectively were used in the analyses. The benthic habitat was quantified with respect to six reef types and two shelf positions (lagoon versus shelf). Spatially-explicit data on the fish assemblage were collected in diver surveys. Multivariate ordination based on fish assemblages and the environmental data did not result in well separated groups of sites. Mapped reef types were not associated with distinct values of either local environmental variables or fish assemblages. Reef types exhibited substantial overlap in ordination plots based on benthic characteristics with groupings based on fish assemblages showing even less pattern. Ordination patterns involving reef type were largely the same for both low and high resolution maps. In contrast, sites showed clear groups for lagoon and shelf in ordinations based on both environmental variables and fish assemblage composition respectively. These results suggest that knowledge of the overall fish

assemblage or fine-scale environmental characteristics could not be used to predict reef type or vice versa.

Introduction

The vast majority of ecological studies of reef fish to date have focused on documenting and understanding links between the fish assemblages observed and local environmental variables measured at sub-meter scales. For example, associations have been reported between fish abundance, distribution, and assemblage structure and local variables such as live coral (Roberts and Ormond 1987, Chabanet et al. 1997, Garpe and Öhman 2003), turf algae (McAfee and Morgan 1996, van Rooij et al. 1996), reef rubble (Itzkowitz 1977, Bruggenmann et al. 1994), macroalgae (Lawson et al. 1999), and rugosity (Roberts and Ormond 1987, Booth and Beretta 1994, Friedlander and Parrish 1998, Gratwicke and Speight 2005, Kuffner et al. 2007).

Ecosystem-scale benthic maps have emerged as a key tool in studies of the biology and ecology of coral reefs (Chapter 2, Kendall et al. 2004a, Groeber-Dunsmore et al. 2007), the design of marine protected areas (Christensen et al. 2003, Franklin et al. 2003, Kendall et al. 2004b, Aswani and Lauer 2006, Friedlander et al. 2007), and fisheries management (Ault et al. 2006). Unfortunately, benthic maps often lack sufficient resolution to provide the detailed environmental attributes that have been the focus of most prior studies of reef fish habitat (Diaz et al. 2004). Instead, maps of reef ecosystems are often produced with more general attributes that reflect benthic features depicted at broader scales commensurate with their spectral and spatial limitations as perceived through remote sensing (Chapter 2, Sheppard et

al. 1995, Mumby et al. 1997, Chauvaud et al. 1998, Franklin et al. 2003, Hochberg and Atkinson 2003, Lundblad et al. 2006). In contrast to the highly detailed habitat descriptions that often accompany field studies, benthic maps produced for management, typically delineate reef types in rather general categories simply as “coral” or “reef” or sometimes more specifically as reef rubble, pavement, patch reef, rock reef, and other generalized classes (e.g. FMRI 1998, Kendall et al. 2001, Franklin et al. 2003, NOAA NCCOS 2005, Battista et al. 2007a, b). In addition to this classification discrepancy, the general map categories are defined and depicted as polygons or grid cells at spatial scales much coarser than the sub-meter scales of most studies linking fish to benthic habitat. Little information is currently available to determine whether the broad scales of habitat classification derived from benthic maps that are currently used for management decisions can replace the intensively studied fish/habitat relationships defined at fine scales (Chapter 2, Diaz et al. 2004). The key question for research and management of how well typical map classifications represent local substrate composition or fish assemblages remains largely unanswered.

Three aspects of the previous attempts to address this discrepancy have restricted the inferences drawn: (1) the inclusion of only very general habitat types, (2) the study of a limited subset of a regions reef types or zones, or (3) reef types are defined based on underwater surveys that cannot be readily matched up to those that are able to be defined from remote sensing. For example, some prior studies have focused only on differences between the general map classes such as hard bottom, seagrass, and sand on reef fish assemblages (Ward et al. 1999, Kendall et al. 2004a,

Gratewicke and Speight 2005, Pittman et al. 2007, Christensen et al. 2003, Aswani and Lauer 2006, Friedlander et al. 2007). More specific to hard bottom, all reef types are not equal quality habitat (Crowder et al. 2000) and may play very different functional roles in the ecosystem yet they are grouped in many studies and management considerations. If benthic maps are to be of greatest utility for management, they should be able to quantify differences between specific types of hard bottom (Friedlander and Parrish 1998). For example, patch reefs, uncolonized bedrock, and coral rubble may offer similar habitat in terms of rugosity but may have very different benthic cover types such as live coral and macroalgae that will influence fish assemblage composition. Many prior studies have only examined a small subset of regional reef zones or types. This limits the scope of findings to the particular components of the ecosystem studied. In other studies, reef types are defined from underwater surveys and are often not detectable with remote sensing or able to be efficiently mapped at management scales. This limits application of results to management scales. In other cases, only the best reefs in a region in terms of coral cover are examined due to logistical or design constraints. Such studies are also limited in scope of inference in that a diversity of reef types are present in most regions with the majority of the reef or hard bottom being comprised of “lower quality” hard bottom classes (Franklin et al. 2003, Kendall et al. 2004b) which possess a wide range of dominant cover types and other characteristics. Collectively these limitations have resulted in the need for studies that address a broader spectrum of relationships among fish assemblages, local habitat variables, and the full diversity of reef types able to be mapped in a given ecosystem.

Further complicating matters, the characteristics of benthic maps can vary significantly depending on the spatial resolution of input data or decision rules imposed during mapping (Chapter 2, Capolsini et al. 2003, Andrefouet et al. 2003). For example, the spatial resolution of maps can influence the perceived area, edge length, and number of many common types of reef features (Chapter 2). This has the potential to affect the relationships perceived between mapped features and the fish assemblages associated with the features they represent (Chapter 2).

To overcome the limitations with existing studies noted above, here I seek to understand the relationships among fish assemblages, local habitat variables, and the wider diversity of reef types mapped in a shallow coral reef ecosystem that exhibits a diverse range of physiographies. Specifically, the following questions will be addressed: What are the relationships between fish assemblages and local habitat variables? Can fish assemblages or local environmental characteristics be used to predict the broader reef type? Conversely and more importantly, can reef types identified from remote sensing be used to predict local ecological attributes such as local environmental characteristics or fish assemblages? Does the spatial resolution of maps influence those predictions?

These questions require a multivariate approach given the variability of substrate and cover types that are present in reef ecosystems and the high diversity of species that comprise reef fish assemblages. Recently, multivariate approaches have been effectively used to investigate associations among reef fish species (Auster et al. 2005), changes in reef fish assemblages following major ecosystem alterations (Baron et al. 2004; Garpe et al. 2006), associations between fish assemblages and reef

characteristics or zones (Alevinson et al. 1985; McGehee 1994; Öhman and Rajasuriya 1998; Garpe and Öhman 2003; Beger et al. 2003, Arias-Gonzalez et al. 2006), and similarity patterns among reefs based on local environmental data (Harriott et al. 1994; Valesini et al. 2003).

Here, I used multivariate analyses to test the following hypotheses:

- 1) Local environmental variables can predict fish assemblages on coral reefs. If a significant correlation exists, a subset of the local habitat variables will best explain the patterns in fish assemblage structure.
- 2) Clusters of a) local environmental variables and b) fish assemblages can be defined statistically that reflect discrete reef types.
- 3) A priori classifications of reef types and geomorphological zones in benthic maps can be statistically discriminated by a) local environmental characteristics and b) fish assemblages.
- 4) Results of 3 a and b will be influenced by spatial resolution (high versus low) of benthic maps.

Methods

The study was based on the marine landscape and fish assemblages around Buck Island Reef National Monument (BIRNM), US Virgin Islands (Figure 3.1). The area has been intensively mapped and characterized for National Park Service monitoring and as part of the US Coral Reef Task Force's initiative to produce consistent shallow water coral reef ecosystem maps for all US states and territories (USCRTF 1999). Characterization at BIRNM has included a diver-based survey of

fish assemblages and local benthic characteristics as well as application of remote sensing to produce benthic maps at multiple scales as described in subsequent sections.

Fish Survey Data

Visual diver-based surveys were used to census both the fish and bottom features within and around BIRNM. Between 2002 and 2006, 588 sites were selected for study based on a randomly stratified design. Sampling was generally distributed evenly between a spring season (March) and fall season (October) each year. The sampling design around BIRNM was devised to address NPS monitoring needs inside versus outside of park boundaries. The monitoring design resulted in independent survey sites spread widely in the study area each within one of the six types of hard bottom identified from benthic maps. Sampling effort was distributed in proportion to the area of each of the six hard bottom types. At each of these sites a diver swam along a randomly selected compass heading and surveyed a 25*4 meter transect (100 m²). Divers recorded the species and abundance of all fish observed. Diver swimming speed was maintained to conduct the survey in ~15 minutes regardless of substrate type or complexity.

Preliminary analyses of the data included 185 fish species. However, the distribution of abundances per species per site was highly skewed. Sites with unusually large schools of fish or rarely seen species obscured the more general similarity patterns in fish assemblages, issues which no data transformations could acceptably alleviate. Because the objective was to characterize general fish assemblages rather than rare fish or extreme observations, very large schools of

individual fish species were capped at 100 individuals. Also removed were rare species not seen at a minimum of 5% of the sites (123 species removed, 27 of which were represented by a single individual in the data base) (Clark and Warwick 2001). This restricted analysis to those species with enough observations to produce patterns that are detectable and stable. Removal of extreme observations enabled discrimination of the more general differences among fish assemblages. These steps resulted in 62 species for analysis.

Benthic Survey Data

In addition to the fish census at each survey site, divers conducted a detailed characterization of benthic habitats. A 1-m² quadrat, divided into 100 smaller squares (10 x 10cm), was used to estimate percent cover at five stratified and randomly selected separate positions along the 25 m transect. Quadrat locations were distributed such that there was one random point within every 5 m interval along the transect. Two-dimensional percent cover of bottom types was visually estimated within each quadrat from directly above. Biotic variables recorded within the quadrat were the percent cover of macroalgae, turf algae, live corals, and other biota (e.g. sponges, soft corals, tunicates, anemones, zooanthids, and hydroids). Abiotic variables recorded within quadrats were the percent cover of softbottom (sand and finer sediments) and hardbottom (rubble, rock, and coral). Percent cover measurements within the quadrats of a given transect were averaged to obtain single values for each survey site. Depth and rugosity were recorded. Depth was measured to the nearest meter at each quadrat using the divers' depth gauge. Rugosity was measured by draping a 6-m long chain at two randomly selected positions along the 25m belt transect. The chain was placed

such that it followed the substrate's relief along the centerline of the transect. The straight-line horizontal distance covered by the chain was measured, divided by 6 (m), and then subtracted from 1 to determine rugosity. As a result, rugosity was a value between zero and one. The two values of rugosity for each transect were averaged into a single value for each survey site. The following variables were used in the multivariate analysis; soft bottom cover, depth, live coral cover, macroalgal cover, turf algal cover, and rugosity since prior research indicated that these were the most important variables of fish habitat (e.g. Itzkowitz 1977, Roberts and Ormond 1987, Chabanet et al. 1997, McAfee and Morgan 1996, Friedlander and Parrish 1998, Garpe and Öhman 2003, Gratwicke and Speight 2005, Kuffner et al. 2007). Incompletely surveyed sites that did not have values for all environmental variables were eliminated resulting in 495 sites available for analysis.

Benthic Maps

Maps used in this study have spatial and thematic resolution consistent with those produced for regional mapping in many parts of the world including the US Caribbean (Kendall et al. 2001), Hawaii (Battista et al. 2007a), Florida Keys (FMRI 1998), American Samoa, Guam, Mariana Islands (NOAA NCCOS 2005), and Palau (Battista et al. 2007b). Two benthic maps of the BIRNM area based on two levels of spatial resolution were considered for this analysis (Full details provided in Chapter 2). Maps were created from orthorectified aerial photographs and visual interpretation using GIS software (Kendall et al. 2001). A relatively large minimum mapping unit (MMU, size of the smallest feature to be mapped) of 4047 m² (1 acre) and a much smaller MMU of 100 m² (0.0247 acre) were used to create the two

separate maps (Figure 3.2). The classification scheme used to attribute maps at both spatial scales included a total of six hard bottom or reef categories as defined by a group of local scientists. These six categories were linear reef, patch reef, colonized pavement (col. pav.), scattered coral and rock in sand (scattered c & r), colonized bedrock (col. bedrock), and reef rubble (Kendall et al. 2001). In addition to these bottom types, shelf zones were identified that split hard bottom habitat into two groups, lagoon and shelf. These represent distinct geomorphological regions of reef ecosystems thought to influence biotic distributions and that typically consist of nearshore, low energy and offshore, higher energy areas respectively. Zones are large features that were insensitive to change in MMU (at the two spatial scales considered here) and therefore did not differ spatially between the two maps. The categories and spatial scales used are representative of typical spatial resolutions presently used to produce maps of reef ecosystems. For the multivariate analysis, the positions of the fish survey sites were overlaid on the two benthic maps respectively and the reef type and zone corresponding to the site coordinates were recorded.

Multivariate Analyses

Analyses were conducted primarily using the software Primer-E v6.0.2 (Clark and Warwick 2001). The statistical analyses conducted to test each hypothesis are described below.

Hypothesis 1. Local environmental variables (sub-meter scales) can predict fish assemblages on coral reefs. If a significant correlation exists, a subset of the local habitat variables will best explain the patterns in fish assemblage structure.

Two suites of analysis were conducted to test this hypothesis. Prior to analysis, depth was log transformed and all other habitat variables (original values were either percentages or proportion) were square-root transformed. The fish abundance data were square-root transformed. This was done to moderately downplay the dominant influence of very common species (Clark and Warwick 2001). We constructed two Bray-Curtis similarity matrices that expressed the relative similarity between 495 sites with respect to their local environmental variables and the fish assemblages respectively. The strength of association between these two matrices was determined by rank correlation (Spearman's ρ) between habitat and fish assemblage patterns. Once the correlation between these matrices was calculated, a permutation test was applied wherein site labels were randomly reassigned to determine the probability that the measured correlation between the two matrices arose by chance. Analysis was conducted using 999 permutations and the RELATE procedure in Primer (Clark and Warwick 2001).

Subsequently, I analyzed what local habitat variables were most important for explaining the pattern in the fish assemblage observed at each site. To conduct these analyses all habitat data were transformed as previously described and then normalized using Z-score transformations (Clark and Warwick 2001). Spearman rank correlation (ρ) was calculated between the fish assemblages and all possible combinations of habitat variables and the ten models with highest values were identified. The significance of the highest correlation was tested against a null hypothesis of no agreement in multivariate pattern between habitat variables and fish assemblages. A permutation test was used wherein sample labels were randomized

and correlations calculated 99 times to determine the probability that the observed highest correlation could have arisen by chance. This number of permutations enabled calculation of a p-value to the hundredths digit while keeping computation times reasonable. Analysis was conducted using the BIOENV procedure within Primer.

Hypothesis 2) Clusters of a) local environmental variables and b) fish assemblages can be defined statistically that reflect discrete reef types.

We used an ordination procedure to determine if sites could be meaningfully grouped based on multiple local environmental characteristics. Non-metric Multidimensional Scaling (MDS) was selected because this technique plots the similarity between samples based on their distance from each other in multivariate space. Preliminary analyses indicated that results using all 495 survey sites produced ordinations with extensive overlaps among sites. This large number of sample sites is generally considered to be too many to allow interpretable relationships (Clarke and Warwick 2001). Therefore, the 495 surveys were split randomly into five subsets of equal size ($n = 99$) without replacement. For each of the five subsets, MDS was conducted on Bray-Curtis similarity matrices calculated from Z-score normalized data (Clarke and Warwick 2001). Normalization converted the habitat variables into a common scale, a necessary step for MDS. To visualize the influence of the local habitat variables on the MDS, individual bubble plots for the following variables were created; depth, rugosity, and cover of soft bottom, live coral, macroalgae, and turf algae wherein point size indicates variable value.

Similar analyses were conducted using the fish assemblage data as input to the analysis to determine if sites could be meaningfully grouped based on the relative similarities of their overall fish assemblages. The same five subsets of sites used in the MDS based on local habitat variables were used. For each of the five subsets, MDS was conducted on Bray-Curtis similarity matrices and untransformed data (Clark and Warwick 2001). Plots based on square-root transformed fish data, used in hypothesis 1, yielded similar results to those based on untransformed data but increased stress values of plots. To visualize the influence of the local habitat variables on the MDS based on fish assemblages, bubble plots for the local habitat variables were created; depth, rugosity, and cover of soft bottom, live coral, macroalgae, and turf algae.

Hypothesis 3) A priori classifications of reef types and geomorphological zones in benthic maps can be statistically discriminated by a) local environmental characteristics and b) fish assemblages.

I tested the null hypothesis that there was no difference among map categories (i.e. reefs types or geomorphological zones) based on their local environmental characteristics. This analysis was conducted on standardized data and the Bray-Curtis similarity matrix for habitat data. Three separate analyses were performed using the map variables associated with each of the 495 survey sites. These variable groups were geomorphological zone (lagoon or bank/shelf), reef type from low resolution maps (6 types), and reef type from high resolution maps (6 types). Analyses were conducted using permutation tests in a fashion analogous to analysis of variance using the ANOSIM procedure in Primer. Using permutation tests, the significance of a

global test statistic (R) among all groups is calculated using rank similarities.

Following that, all pairwise comparisons between zones or reef types are calculated along with their respective R values and significance. The statistic R is scaled such that a value of 0 indicates no differences among groups and a value of 1 indicates that dissimilarity of sites in different groups is always larger than dissimilarity of sites in the same group.

To visualize correspondence with classifications in benthic maps, MDS of sites based on local habitat variables (from Hypothesis 2a) were coded as factor plots using the map attributes: bottom type from low resolution map, bottom type from high resolution map, and geomorphological zone.

In addition, to aid interpretation of the MDS and ANOSIM results, it was desirable to quantify how the six reef categories in low and high resolution maps, as well as reef zones, differed in their local environmental characteristics. Observations from different individual sites that were classified as belonging to the same reef type or zone were considered replicates in these analyses. To test for differences among reef types for each variable, ANOVA, followed by Tukey-Kramer multiple means comparisons were conducted using the statistical software JMP v6. Depth was log-transformed and all other variables were square-root-transformed prior to statistical tests to meet assumptions of normality and equality of variance. The mean and standard error of each variable and reef type were plotted in untransformed values and marked for significant differences.

We also tested the null hypothesis that there was no difference among groups (i.e. reefs types or geomorphological zones) based on their fish assemblages. The

analysis was conducted on square root transformed fish abundance data and the resulting Bray-Cutis similarity matrix. As with the analysis based on habitat variables, three separate analyses were performed using the map variables associated with each fish survey site. These variable groups were geomorphological zone, reef type from low resolution maps, and reef type from high resolution maps. The ANOSIM procedure in PRIMER was used to test this hypothesis.

To visualize correspondence with classifications in benthic maps, MDS of sites based on fish assemblages (from Hypothesis 2b) were coded as factor plots using the map attributes: bottom type from low resolution map, bottom type from high resolution map, and geomorphological zone.

Hypothesis 4) Results of 3 a and b will be influenced by spatial resolution (high versus low) of benthic maps.

The two MDS plots based on local environmental characteristics and labeled with reef types from low and high resolution maps respectively were compared for similar patterns. In addition, the results of the pairwise ANOSIM analysis (Hypothesis 3a) of reef types were compared for similar patterns when based on low versus high resolution maps. The results of the MDS and ANOSIM analysis based on fish assemblages (Hypothesis 3b) were evaluated for differences due to map resolution in similar fashion.

Results

Hypothesis 1) Local environmental variables can predict fish assemblages on coral reefs. If a significant correlation exists, a subset of the local habitat variables will best explain the patterns in fish assemblage structure.

There was a significant relationship between the similarity matrices created for sites based on habitat variables and fish abundances ($\rho = 0.2$). None of the 999 random permutations resulted in a correlation equal to or greater than the measured value of 0.2, indicating that the correlation was significant at the $p < 0.001$ level.

The BIOENV procedure indicated that a three variable model that included soft bottom cover, depth, and rugosity best explained the pattern in similarity among fish assemblages ($\rho = 0.428$, $p < 0.01$) (Table 3.1). Depth was included in all of the ten-best models examined. The percent coverage of soft-bottom and live coral occurred in 8 and 7 of the ten-best models, respectively. Percent cover of macroalgae and turf algae were the least used variables in a list of the ten best models explaining the fish assemblages.

Hypothesis 2) Discrete reef types can be identified based on: a) local environmental variables, and b) fish assemblages.

The MDS ordinations identified clear gradients in local environmental variables among plots. The overall ordinations were strong with low stress values of ~ 0.14 (Clarke and Warwick 2001). All five random subsets of data showed similar patterns and stress levels, therefore only one is shown here for brevity. Sites plotted in one large group rather than clustered in separate areas of the MDS plot (Figure 3.3).

This indicates that there was a gradient in similarity based on habitat variables rather than well separated groups. Variables that showed clear patterns in the MDS ordination space using bubble plots were depth, soft bottom cover, and turf algae with a marginal separation shown for rugosity. Cover of live coral and macroalgae showed no clear patterns in the ordination space (Figure 3.3).

The MDS plots based in fish assemblages had relatively high stress values of ~0.21-0.23 which indicates a marginal ordination (Clarke and Warwick 2001). All five random subsets of data showed similar patterns and stress levels, therefore only one representative ordination is shown (Figure 3.4). The ordination pattern indicates that there was more of a continuum in similarity among sites based on fish assemblages rather than well separated groups. Only survey depth showed a clear pattern of correspondence among sites in the MDS ordination space using bubble plots of the environmental data (Figure 3.4). Three defined but adjacent groups were observed. Rugosity also indicated a perceptible correspondence with the similarity among fish sites. No clear patterns of correspondence were seen with any of the cover variables.

Hypothesis 3) A priori classifications of reef types and geomorphological zones in benthic maps can be statistically discriminated by a) local environmental characteristics.

Geomorphological Zone (same for both map resolutions)

The MDS plot coded by shelf zone showed a clear separation into sites in lagoon and those on the shelf (Figure 3.5). While there were two clear groups based

on this factor, the groups were adjacent to each other with some overlap rather than well separated in ordination space.

The ANOSIM indicated a significant difference between lagoon and bank/shelf sites based on their habitat characteristics ($R = 0.258$, $p < 0.001$). The companion parametric analysis revealed that the two shelf zones differed in only three of the six local environmental characteristics evaluated (Figure 3.6). Shelf sites were significantly deeper and had a significantly lower percent cover of soft bottom and macroalgae than those in lagoons.

Reef types from low resolution maps

The overall ANOSIM for a difference among any of the reef types mapped at low resolution based on their local habitat variables was significant ($R = 0.068$, $p = 0.01$). This warranted examination of the pair-wise tests between bottom types to determine which differed based on local habitat variables. Due to the large number of permutations performed it was found that many comparisons yielded significant differences between pairs of reef types but that values were ecologically minor (i.e. $R < \sim 0.3$). An R of 0 indicates very similar values of local environmental variables between reef types whereas an R of 1, the largest possible, indicated completely different values for local variables between reef types. Eight of the fifteen pair-wise comparisons between reef types were significantly different; however, many had low R values and were not likely to be ecologically meaningful (Table 3.2). Two comparisons, Scattered Coral & Rock versus Colonized Bedrock and Reef Rubble versus Colonized Bedrock, had much higher R values well separated from the rest.

The companion parametric analysis showed that reef types depicted in low resolution maps showed many significant differences in local environmental characteristics (Figure 3.7). Colonized bedrock and linear reef had significantly shallower mean depth (5-10 m) than other reef types (27-38 m). Percent cover of soft bottom was significantly higher in the scattered coral and rock category (40%) than for all other reef types (6-17%) except reef rubble. Mean percent cover of live-coral was highest for patch reefs (15%), significantly higher than for colonized pavement, reef rubble, and scattered coral and rock. Mean percent cover of macroalgae was significantly higher on linear reefs (15%) than on colonized pavement (10%) but was indistinguishable among other reef types. Mean cover of turf algae was significantly higher on colonized bedrock (57%) and pavement (49%) than on scattered coral and rock (27%) but was indistinguishable among other reef types. Mean rugosity was significantly higher on patch reefs (0.3) than on colonized pavement and scattered coral and rock but was indistinguishable among other reef types.

Reef types from high resolution maps

The overall test for a difference among any of the reef types mapped at high resolution based on their local habitat variables was significant ($R = 0.126$, $p < 0.001$). This warranted examination of the pair-wise tests between bottom types. Six of the fifteen pair-wise comparisons between reef types were significantly different; however, four had low R values and were not likely to be ecologically meaningful (Table 3.3). As with the results for reef types mapped at low spatial resolution, two comparisons, Scattered Coral & Rock versus Colonized Bedrock and Reef Rubble

versus Colonized Bedrock, had much higher R values that were well separated from the rest.

The companion parametric analysis showed that reef types depicted in high resolution maps also showed significant differences in many local environmental variables with patterns broadly similar to those quantified for low resolution maps (Figure 3.8). Colonized bedrock and linear reefs were significantly shallower than most other reef types. Patch reefs occurred more at intermediate depths, significantly shallower than colonized pavement and reef rubble. Again, scattered coral and rock showed significantly higher percent cover of soft bottom than other reef types. The largest contrast between map resolutions was for percent cover of live coral. No significant differences in live coral cover were found among any reef types mapped at high resolution whereas several significant differences were found for reef types mapped at low resolution. Mean percent cover of macroalgae was significantly higher on patch reefs than on colonized pavement but indistinguishable among other reef types. Mean cover of turf algae was significantly higher on colonized pavement and patch reefs than on scattered coral and rock but was indistinguishable among other reef types. Mean rugosity was significantly higher on patch reefs than on either colonized pavement or scattered coral and rock.

When sites were coded in factor plots with the corresponding reef type from benthic maps, no clear patterns were evident. Whether derived from the high or low resolution map (Figure 3.9), reef types were spread throughout the MDS plots for local habitat characteristics with lots of overlap in the distribution of mapped categories.

Hypothesis 3) Individual reef types and geomorphological zones, as identified in benthic maps (low and high resolution respectively), possess distinct: b) fish assemblages.

Geomorphological Zone (same for both map resolutions)

A significant difference was found between lagoon and bank/shelf sites based on their fish assemblages ($R = 0.345$, $p < 0.001$). The MDS plot coded by shelf zone showed clear groupings of the sites in the lagoon versus those on the shelf (Figure 3.10). While there were two clear groups based on this factor, the groups were adjacent to each other with a small amount of overlap rather than well separated in ordination space.

Reef types from low resolution maps

The overall test for a difference among any of the reef types mapped at low resolution based on their fish assemblages was significant ($R = 0.207$, $p < 0.001$). This warranted examination of the pair-wise tests between bottom types. Thirteen of the fifteen pair-wise comparisons between reef types yielded significant differences; however, most had low R values and were not likely to be ecologically meaningful (Table 3.4). Only five of the pair-wise comparisons had higher R values, these were well separated from the rest.

Reef types from high resolution maps

The overall test for a difference among any of the reef types mapped at high resolution based on their fish assemblages was significant ($R = 0.177$, $p < 0.001$).

This warranted examination of the pair-wise tests between bottom types. Twelve of the fifteen pair-wise comparisons between reef types were significantly different; however, most had low R values and were not likely to be ecologically meaningful (Table 3.5). Only four of the pair-wise comparisons had higher R values, these were well separated from the rest.

Similar to the results of the habitat data, when sites were coded in factor plots with the corresponding bottom type from benthic maps, no clear patterns were evident. Whether derived from the high or low resolution map (Figure 3.11), reef types plotted according to similarity in fish assemblages were spread throughout the MDS plot with lots of overlap in the distribution of categories.

Hypothesis 4) Results of 3 a and b will be influenced by spatial resolution (high versus low) of benthic maps.

The MDS plots of sites based on local environmental variables coded by the low versus high resolution benthic maps respectively showed very little difference (Figure 3.9). This suggests that both map resolutions yielded similar results in these analyses. This was supported by comparison of the ANOSIM results for both map resolutions (Tables 3.2 and 3.3). The same reef types were found to differ for low and high resolution maps.

Only minor differences were found due to map scale for analyses based on fish assemblages. The MDS plots of sites based on fish assemblages coded by the low versus high resolution benthic maps respectively showed little difference (Figure 3.11). The primary difference between plots was a diffuse cluster of colonized pavement sites in the high resolution map that was instead coded as patch reefs in the

low resolution map. Overall however, both map resolutions yielded similar results showing much overlap in similarity among reef types. This was supported by comparison of the ANOSIM results for both map resolutions (Tables 3.4 and 3.5). Many of the same reef types were found to differ for low and high resolution maps.

Discussion

The relationships among local habitat variables, fish assemblages, and mappable reef types presented here provide links between the many prior studies of fine-scale habitat utilization patterns of fish to broad-scale benthic maps. Multivariate analyses indicated that the local habitat variables that best explained fish assemblage composition at BIRNM were depth, rugosity, live coral, and soft bottom cover. This was not unexpected given that similar suites of variables were identified in prior multivariate-based studies of reef fish assemblages in other regions (e.g. structural complexity in Öhman and Rajasuriya 1998, depth and live coral in Garpe and Öhman 2003, depth in Arias-Gonzalez et al. 2006, live coral in Garpe et al. 2006). The results here are based on actual abundance values of the respective species encountered. Other studies based on the comparable but simplifying summary metric of fish diversity have also found good correlations (60-90%) with a similar suite of variables including topographic complexity/rugosity (Risk 1972, Öhman and Rajasuriya 1998, Chabanet et al. 1997, Friedlander and Parrish 1998), coral cover (Chabanet et al. 1997, Öhman and Rajasuriya 1998) and depth (Friedlander and Parrish 1998).

The convergence of the results reported here and those of other studies on the ability of a subset of key fine-scale habitat variables to explain fish assemblage

structure indicates progress toward understanding environmental influences on assemblage structure of reef fish. Unfortunately, these multivariate relationships cannot be readily implemented for predicting fish distributions over broad regions since all of these habitat variables are not presently detectable from remote sensing at the required spatial scales (Diaz et al. 2004). For example, estimates of both rugosity and depth derived from remote sensing have had mixed success in matching values of those variables as measured under water (Kuffner et al. 2007, Wedding et al. 2008). Estimates of the percentages of specific cover types such as live coral can be mapped with ever-increasing detail and may soon be detectable at scales similar to those measured by divers (Hochberg et al. 2003, Isoun et al. 2003). As technologies such as high resolution satellites, hyperspectral sensors, lidar, and multibeam sonar improve, estimates derived from such measurements may achieve the precision and accuracy required to enable knowledge of the distribution of fine-scale environmental variables across entire landscapes to be used to predict fish assemblages. However, the analyses presented here indicate that until then, current technologies limit the ability to understand relationships between fish, local habitat variables, and the more general reef types at broad spatial scales. Overcoming these limitations remains a priority for research and management.

Multidimensional scaling analysis did not result in clear separation of either the fish assemblages or the environmental data at BIRNM. This indicates that, rather than distinct groupings, a continuum of local fish and environmental conditions exists among the reef types across the study area. In MDS plots based on local habitat variables at BIRNM, a subset of the habitat variables drove the similarities among

sites. Depth, rugosity, turf algae, and soft bottom cover showed clear gradients along independent axes of the ordination space.

Several prior studies have used similar multivariate approaches to identify the local habitat variables responsible for differences in predefined reef types in other regions. Six nearshore marine habitats off SW Australia identified by subjective visual assessment did not separate well in ordination space until a subset of environmental variables (cover of sand, reef, and seagrass plus four landscape measurements) was identified that provided the best quantitative discrimination among habitat types (Valesini et al. 2003). Six pre-defined reef types, identified from coarse preliminary surveys, in the northern Indian Ocean were found to differ from each other based on live coral cover, substrate diversity, sand cover, and structural complexity (Rajasuria et al. 1998). Three reef types investigated in the waters off East Africa yielded groups in ordination plots according to replicates within a reef site but, similar to results presented here, did not form separate groups according to reef type (Garpe and Öhman 2003).

Some prior studies yielded better discrimination of reef types based on local environmental data than those observed here for the reef ecosystem at BIRNM. Two differences in methodology probably contribute to an apparently improved separation of reef types in some studies: non-random site selection and pre-classification of reef types from *in situ* observation rather than through remote sensing. Non-random site selection and sometimes intentional maximization of the local environmental differences in reefs selected for survey can enable specific comparisons but limits scope of inference to the chosen sites rather than the wider ecosystem (e.g. Harriott et

al. 1994, Chabanet et al. 1997, Arias-González et al. 2006). This will result in better separation of groups in statistical ordinations, but this separation will represent patterns in site selection rather than the overall underlying ecological structure. Similarly, observation of reef sites under water (in contrast to remotely sensed) enables identification of reef types with differing local characteristics that would enhance group separation in MDS. While the general reef types predefined in these prior studies were not based on mapping, as was the case in our study, the results are analogous and demonstrate that a subset of 4-7 environmental variables can be used to at least partially distinguish among a similar number of reef types. When survey sites are randomly scattered in reef types however, a continuum, rather than a clearly separated suite of characteristics appears to differentiate reef classes.

Ordination analyses of the fish assemblages at BIRNM were relatively uninformative. Only depth showed a clear pattern with three well defined groups of sites with respect to their fish assemblages. Multivariate studies of fish assemblages in other areas have yielded similarly mixed results. McGehee (1994) found depth to be a factor influencing assemblage structure on fore reefs in SW Puerto Rico using cluster analysis and DCA. Arias-Gonzales et al. (2006) also found a depth-based segregation of 3 reef fish assemblages in eastern Australia, although groups were less defined than our results at BIRNM. Öhman and Rajasuriya (1998) found very discrete reef fish assemblages in two of six reef types studied off Sri Lanka and grouped but overlapping assemblages in four others. Garpe and Öhman (2003) found that replicate surveys of fish within a reef site grouped reasonably well in ordination plots but reef

types did not. Overall these studies suggest that fish assemblages can be less consistently differentiated than local environmental features.

The few patterns observed in fish versus habitat-based ordinations at BIRNM were not consistent. Stations simply grouped differently depending on whether fish or benthic variables were used. Beger et al. (2003) found greater spatial heterogeneity among reefs off Papua New Guinea based on fish assemblages than corals. An inshore/offshore gradient of three types of fish assemblages did not exhibit a significant correlation with corals at the same sites which plotted instead in one large group with several unique outliers. Chabanet et al. (1997) found similar results using correspondence analysis and dynamic clustering of reef stations. While four substratum classes or reef types were found, they did not appear to directly correlate with fish assemblage structure. Arias-Gonzalez et al. (2006) and Öhman and Rajasuriya (1998) also found that fish – substrate relationships varied by reef type. In contrast, Garpe and Öhman (2003) found reasonably good correspondence between ordination patterns based on benthic versus fish assemblages. The results at BIRNM and those of other studies in general suggest that reef types group more loosely by their fish assemblages than by local habitat characteristics. For example, Garpe and Öhman (2003) found that groups in MDS were more dispersed when based on fish assemblages relative to the more compact groupings that resulted from MDS based on benthic variables. Perhaps the mobility of and size-specific habitat use by fish, in contrast to sessile biota, results in more diffuse ordination results.

In general, mapped reef types were not associated with distinct values of either local environment or fish assemblage. Even though survey sites were randomly

spread over hard bottom, it was expected a priori that the discrete reef types in benthic maps would be characterized by distinguishable fine-scale environmental characteristics and that they would also harbor fish assemblages more similar within than among reef types. However, only modest grouping of reef types was evident with large amounts of overlap among sites, a finding similar to recent comparisons of Hawaiian fish assemblages on colonized versus uncolonized hardbottom (Friedlander et al. 2007). This further suggests that the benthic characteristics and fish assemblages are actually quite similar among most reef types and differ along gradients rather than more discretely.

Despite broad similarities, a few of the specific reef types were significantly different from each other. Colonized bedrock was distinguished from scattered coral and rock and reef rubble largely on the basis of depth, algal cover, and soft bottom cover. Reef rubble had a different fish assemblage than linear reefs, patch reefs, and colonized bedrock. These patterns were largely the same for both low and high resolution maps which indicates an overall robustness of comparisons involving the detailed attributes of reef types mapped at different scales. This was not completely expected given that many of the reef types considered in this study have significantly different landscape properties in terms of area, perimeter, shape index, and neighborhood characteristics (Chapter 2). Significant differences in landscape properties among reef types apparently do not translate into differences in fine-scale benthic characteristics or overall fish assemblages. The most noticeable difference due to map scale was that a group of sites mapped as patch reefs at low resolution were mapped as colonized pavement at high resolution (Chapter 2). These appeared

in a distinct area of the MDS plot based on abundance of fish species indicating a difference in their corresponding fish assemblages.

In contrast to the inability to detect differences among reef types at BIRNM, discrimination of reef physiography and fish assemblage composition based on geomorphological zone was possible. While clearly distinct, the lagoon and shelf groups were adjacent to each other in our ordinations and therefore the differences between the two zones may represent a continuum rather than being entirely different. Environmental variables responsible for the difference were depth, macroalgae, and soft bottom cover. Not surprisingly, lagoons were shallower and had greater cover of macroalgae and soft bottom as would be expected for nearshore sheltered habitats. Fish assemblages between lagoons and shelf environments at BIRNM have been shown to differ in proportional abundance of zooplanktivores and herbivores (Kendall et al. 2004b). The assemblage outside the lagoon has a higher proportional abundance and number of zooplanktivorous species potentially to take advantage of higher current flow and hence food availability (Kendall et al. 2004b). In contrast, the fish assemblage inside the lagoon has a higher proportional abundance of herbivores perhaps due to the greater forage base of macroalgal cover in that reef zone (Kendall et al. 2004b). Garpe and Öhman (2003) showed similarly distinct patterns in not only benthic characteristics but also fish assemblage structure based on the degree of sheltering of reef sites. In French Polynesia, Galzin (1987) found reef zone (i.e. lagoon versus outside the lagoon) to be the largest influence on fish assemblages with less dramatic differences observed between reef assemblages within the same zone. Beger et al. (2003) found three groups of sites in ordinations based on fish

assemblages in reef ecosystems off Papua New Guinea along a gradient from sheltered inshore to exposed offshore sites. McGehee (1994) observed distinct fish assemblages in fore reef (exposed) versus back reef (protected) sides of reefs in Puerto Rico as did Alevizon et al. (1985) in the Bahamas. Christensen et al. (2003) and Kendall et al. (2004b) also looked at the relative effects of habitat type and reef zone on fish assemblages on reefs off Puerto Rico and the Virgin Islands. Although they found habitat type to be a greater influence than reef zone, those studies only looked at three very different habitat types: reef, mangrove, and seagrass. The results of the present study and those of others show that reef zone is more important once individual reef types are included in such analyses.

Rarely have individual reef types derived from benthic maps been comprehensively evaluated for an entire region and had relative comparisons made of their corresponding fish assemblages and benthic characteristics as we have done. Ault et al. (2006) surveyed fish assemblages within 9 reef types mapped and qualitatively defined based on patchiness and vertical relief in waters off Florida. While survey effort in these studies was stratified by reef type, unfortunately data were merged into a single “reef” category for a population assessment, and were not provided for the individual reef types. Aswani and Lauer (2006) compared scientific dive survey data to maps and corresponding benthic assemblages as defined by indigenous people. Correspondence was good, although number of reef types ($n = 2-3$) and spatial scope of the study ($< 2 \text{ km}^2$) were limited. Friedlander et al. (2007) examined fish assemblage biomass on Hawaiian reef ecosystems on colonized versus uncolonized hard bottom areas derived from benthic maps that were similar to those

used in the present study. While statistically significant differences were detected, fish assemblages on the two bottom types were actually quite similar and showed extensive overlap in ordinations. More commonly, reef types or zones are defined from *in situ* surveys rather than from remote sensing (Chabanet et al. 1997, Friedlander and Parrish 1998, Rajasuriya et al. 1998, Valesini et al. 2003, Arias-Gonzales et al. 2006) which limits the transferability of the results to maps and management scales.

Gradients and overlapping groups in habitat variables and fish assemblages appeared to be more the norm than well separated patterns in assemblage composition at BIRNM which can also diminish transferability of results to broad scale benthic maps. In general, the results suggest that one could not use knowledge of the local fish or bottom to forecast reef type or vice versa (but see Arias-Gonzalez et al. 2006). One reason for the high variability and overlap among reef groups in the present study may be that the BIRNM region has suffered repeated and massive stresses in recent years. Centuries of fishing, both traditional and more recently commercial, have profoundly changed Caribbean fish assemblages (Jackson 1997, Rogers and Beets 2001). A formerly dominant reef-building coral species, *Acropora palmata*, was devastated in the 1970s and 80s due to white band disease (Gladfelter et al. 1982, Mayor et al. 2006). In 1983-84 a massive die off of a major algal grazer, the long-spine sea urchin, *Diadema antillarum*, was caused by an unknown pathogen (Lessons et al. 1984, Miller et al. 2003). Over the last several decades a series of major hurricanes have impacted BIRNM (Bythell et al. 1993, Moran and Reaka-Kudla 1991, Rogers et al. 1982). In 2005, widespread coral bleaching was observed, the

effects of which are still being quantified (Clark et al. in press). The combined effects of these events have disturbed the character of the reefs and fish communities severely. Garpe et al. (2006) showed that sites showed wider variability and more dispersion in MDS plots after being disturbed following a bleaching event than undisturbed sites. Arias-Gonzalez et al. (2006) speculated similarly that disturbance events such as bleaching, crown-of-thorns starfish, and storms contributed to the volatility of MDS patterns in fish and benthic assemblage composition. Similarly, differences among the reef types examined in the present study may have been more pronounced prior to the many disturbances that have occurred in the region.

Two lines of future research are most pressing. The goal of the present study was a holistic approach, looking broadly at the fish assemblage rather than at single species or species groups. Results will obviously differ if particular species such as habitat specialists or fish guilds with narrow habitat requirements are analyzed separately (Friedlander and Parrish 1998, Garpe and Öhman 2003, Arias-Gonzalez et al. 2006, Garpe et al. 2006). A useful first step in such analyses would be to determine which species or guilds contribute most to the differences in reef type found in the present study. In addition, the study should also be tested in ecosystems with a range of disturbance. More pristine systems may have greater separation in reef types based on their local environmental variables or fish assemblages. The opposite may be true for heavily disturbed ecosystems. Also important is conducting similar assessments using different types of benthic maps. Vector or raster based maps, discrete or fuzzy classification methods, and sonar, spectral, or laser based

mapping technologies will result in maps with very diverse characteristics that may align differently with local habitat and fish assemblage variables.

All hard bottom or reef types were not created equal (Crowder et al. 2000, Beger et al. 2003), at least when viewed from a broad scale perspective. Indeed the benthic features depicted in the maps used in the present study and those widely produced for other coral reef regions represent distinct reef types with discrete boundaries that can be delineated with high levels of classification accuracy (e.g. Mumby et al. 1997, Battista et al. 2007a, b). When considered at finer scales, however, differences between various reef types are more blurred and less discrete. While some differences were found in local benthic characteristics and fish assemblages among the reef types depicted in benthic maps, the differences were not as distinct or pervasive as initially suspected. Even reef types produced at very different mapping resolution showed similar patterns and a high degree of overlap among fine-scale benthic characteristics and fish assemblages.

Table 3.1: Correlations between fish assemblages and associated environmental variables for the 10 best models resulting from the BIOENV procedure ordered from highest to lowest correlation.

Model	Corr.	No. Vars.	Soft Bottom	Depth	Live Coral	Macroalgae	Turf Algae	Rugosity
1	0.428	3	X	X				X
2	0.427	4	X	X	X			X
3	0.415	3	X	X	X			
4	0.396	2	X	X				
5	0.392	2		X				X
6	0.388	5	X	X	X	X		X
7	0.386	5	X	X	X		X	X
8	0.385	3		X	X			X
9	0.371	4	X	X	X	X		
10	0.369	4	X	X	X		X	

Table 3.2: Pair-wise tests for reef types mapped at **low** spatial resolution. Tests are based on local habitat variables. Significant values of R above ~0.3 are in bold.

Reef type	R	p value
Col. Pavement, Linear Reef	0.136	0.005
Col. Pavement, Scattered C&R	0.147	0.001
Col. Pavement, Patch Reef	-0.033	0.826
Col. Pavement, Reef Rubble	-0.060	0.700
Col. Pavement, Col. Bedrock	0.082	0.120
Linear Reef, Scattered C&R	0.171	0
Linear Reef, Patch Reef	0.124	0
Linear Reef, Reef Rubble	0.117	0.118
Linear Reef, Col. Bedrock	-0.068	0.831
Scattered C&R, Patch Reef	0.141	0
Scattered C&R, Reef Rubble	0.027	0.347
Scattered C&R, Col. Bedrock	0.417	0
Patch Reef, Reef Rubble	0.008	0.444
Patch Reef, Col. Bedrock	0.196	0.004
Reef Rubble, Col. Bedrock	0.635	0

Table 3.3: Pair-wise tests for reef types mapped at **high** spatial resolution. Tests are based on local habitat variables. Significant values of R above ~0.3 are in bold.

Reef type	R	p value
Col. Pavement, Linear Reef	0.159	0.003
Col. Pavement, Scattered C&R	0.175	0.001
Col. Pavement, Reef Rubble	-0.090	0.863
Col. Pavement, Patch Reef	0.044	0.21
Col. Pavement, Col. Bedrock	0.104	0.123
Linear Reef, Scattered C&R	0.131	0.001
Linear Reef, Reef Rubble	0.089	0.119
Linear Reef, Patch Reef	-0.025	0.925
Linear Reef, Col. Bedrock	-0.056	0.752
Scattered C&R, Reef Rubble	0.055	0.19
Scattered C&R, Patch Reef	0.115	0.002
Scattered C&R, Col. Bedrock	0.290	0.001
Reef Rubble, Patch Reef	0.141	0.053
Reef Rubble, Col. Bedrock	0.468	0.001
Patch Reef, Col. Bedrock	-0.022	0.554

Table 3.4: Pair-wise tests for reef types mapped at **low** spatial resolution. Tests are based on fish assemblages. Significant values of R above ~0.3 are in bold.

Reef type	R	p value
Col. Pavement, Linear Reef	0.169	0.001
Col. Pavement, Scattered C&R	0.180	0.001
Col. Pavement, Patch Reef	0.264	0.001
Col. Pavement, Reef Rubble	-0.009	0.553
Col. Pavement, Col. Bedrock	0.270	0.001
Linear Reef, Scattered C&R	0.196	0.001
Linear Reef, Patch Reef	0.200	0.001
Linear Reef, Reef Rubble	0.399	0.002
Linear Reef, Col. Bedrock	0.125	0.042
Scattered C&R, Patch Reef	0.172	0.001
Scattered C&R, Reef Rubble	0.128	0.096
Scattered C&R, Col. Bedrock	0.411	0.001
Patch Reef, Reef Rubble	0.430	0.001
Patch Reef, Col. Bedrock	0.431	0.001
Reef Rubble, Col. Bedrock	0.542	0.001

Table 3.5: Pair-wise tests for reef types mapped at **high** spatial resolution. Tests are based on fish assemblages. Significant values of R above ~0.3 are in bold.

Reef type	R	p value
Col. Pavement, Linear Reef	0.156	0.002
Col. Pavement, Scattered C&R	0.160	0.001
Col. Pavement, Reef Rubble	-0.026	0.64
Col. Pavement, Patch Reef	0.261	0.001
Col. Pavement, Col. Bedrock	0.315	0.001
Linear Reef, Scattered C&R	0.076	0.048
Linear Reef, Reef Rubble	0.300	0.002
Linear Reef, Patch Reef	0.019	0.214
Linear Reef, Col. Bedrock	0.139	0.034
Scattered C&R, Reef Rubble	0.042	0.32
Scattered C&R, Patch Reef	0.133	0.003
Scattered C&R, Col. Bedrock	0.255	0.003
Reef Rubble, Patch Reef	0.320	0.001
Reef Rubble, Col. Bedrock	0.506	0.001
Patch Reef, Col. Bedrock	0.132	0.028

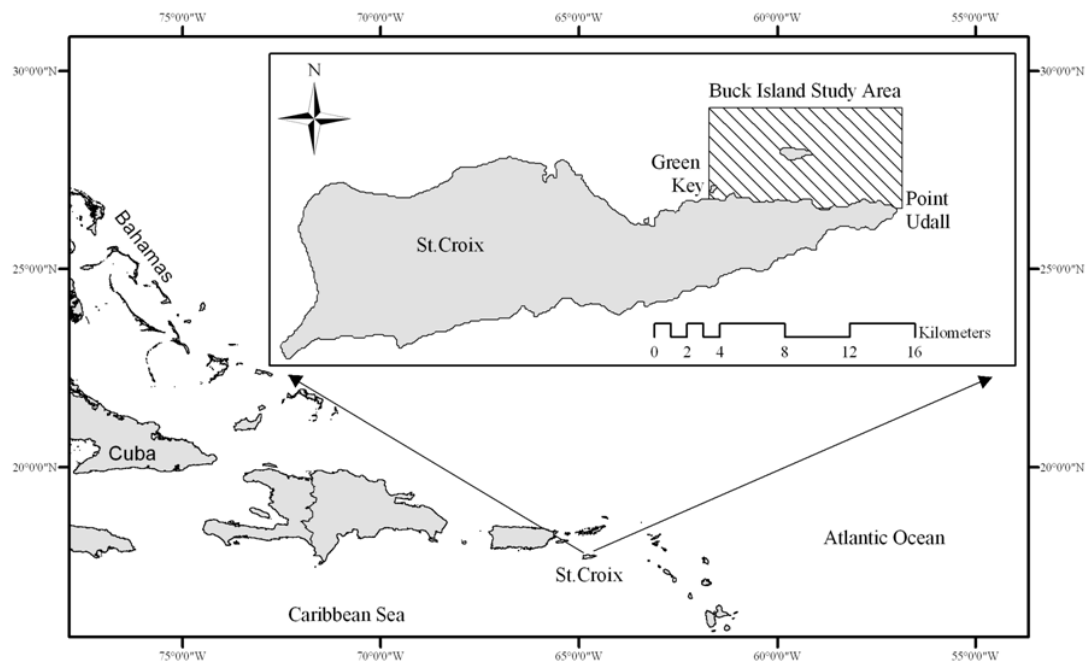


Figure 3.1: Buck Island study area, St.Croix, US Virgin Islands.

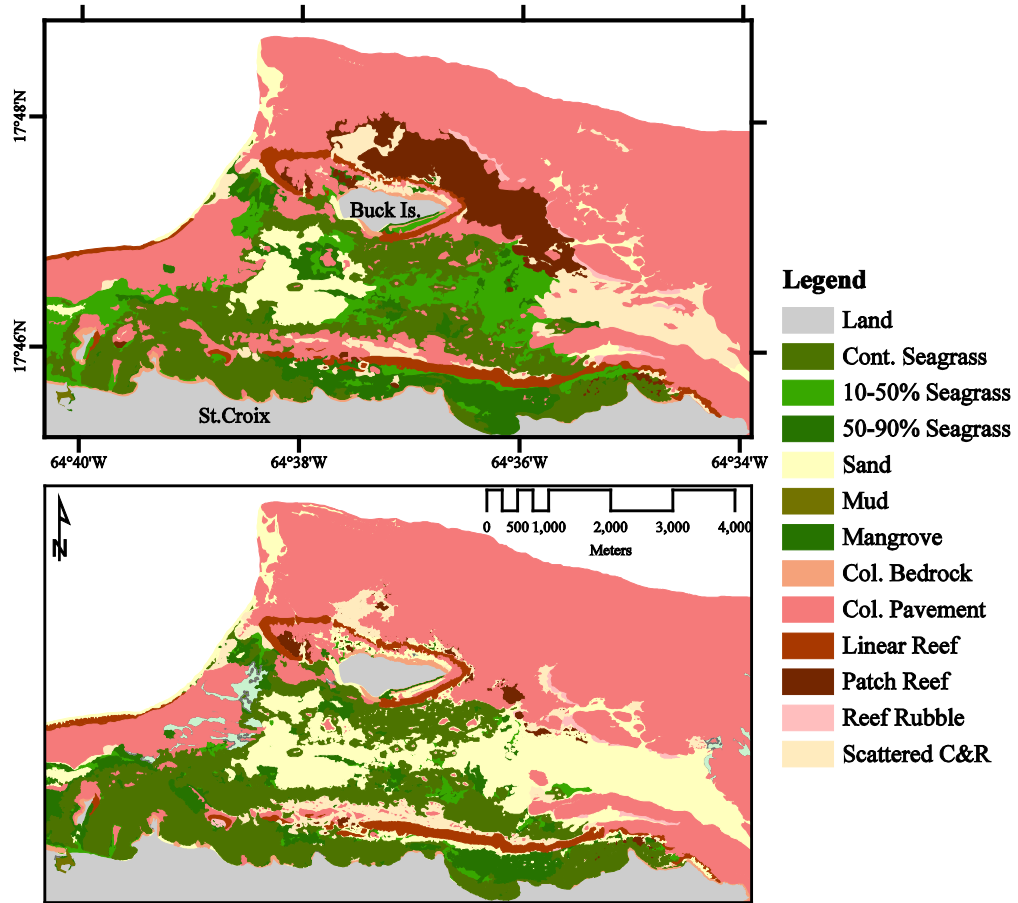


Figure 3.2: Two map types of the study region. Upper map has low spatial resolution (large MMU). Lower map has high spatial resolution (small MMU). White denotes unmapped area beyond the shelf edge.

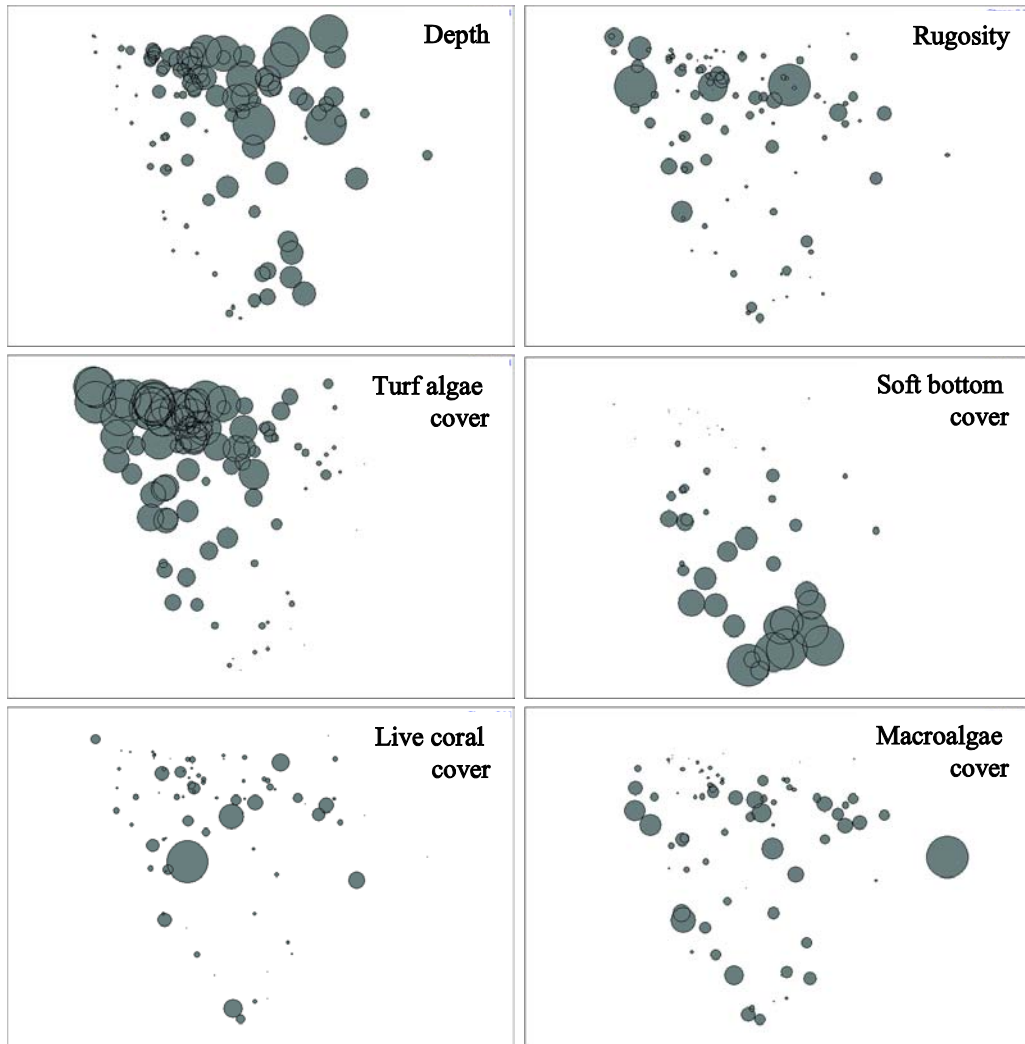


Figure 3.3: MDS of sites by **local habitat characteristics** for one of the five randomly chosen subsets of the survey data (stress = 0.14). Bubble plots are given for each variable where larger circles denote higher cover and rugosity values and deeper depth.

Figure 3.4: MDS of sites by **fish communities** for one of the five randomly chosen subsets of the survey data (stress = 0.22). Bubble plots are given for each variable where larger circles denote higher cover and rugosity values and deeper depth.

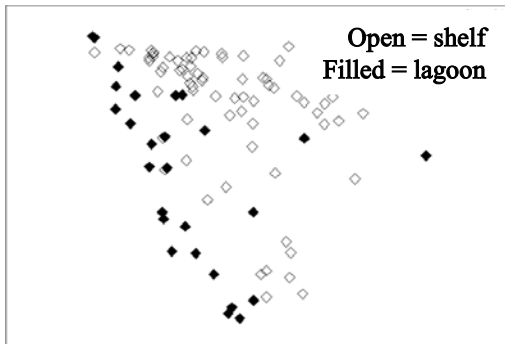


Figure 3.5: MDS of sites by **local habitat characteristics** for one of the five randomly chosen subsets of the survey data (stress = 0.14). Sites are coded by geomorphological zone identified from benthic maps.

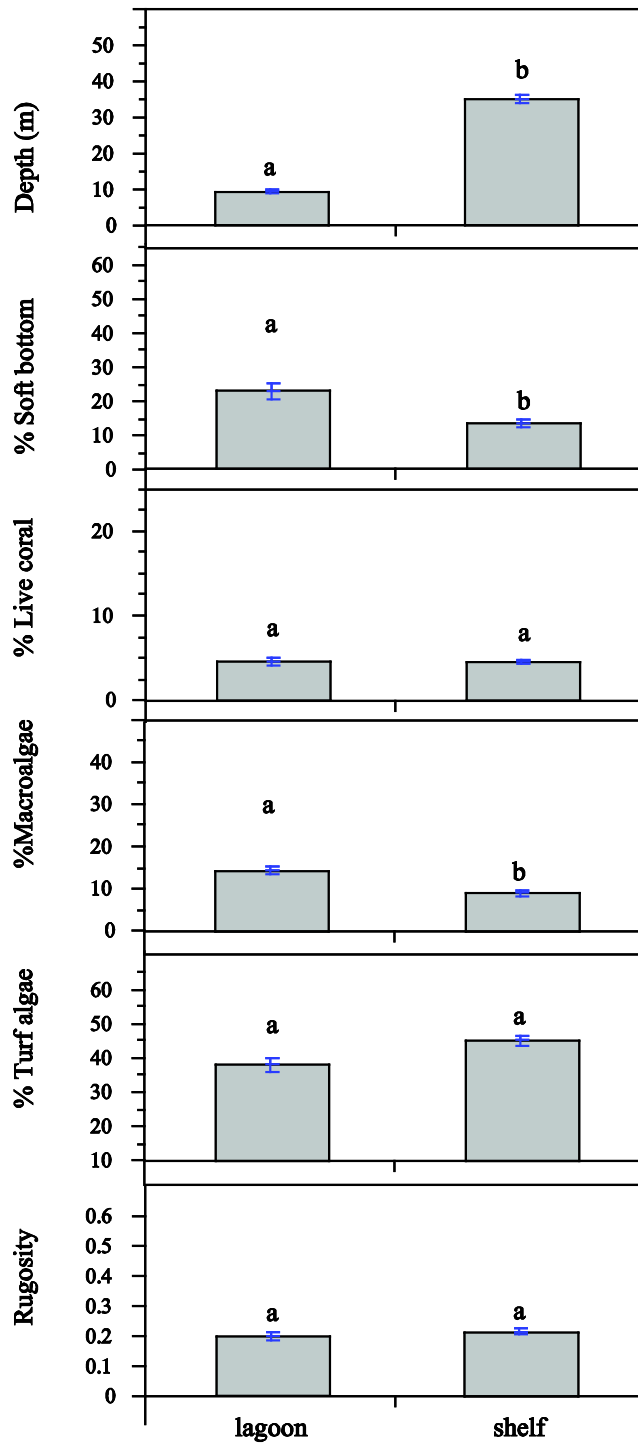


Figure 3.6: Mean (\pm SEM) for **local environmental characteristics** within shelf zones identified from aerial photography. Letters denote pairs with significant differences in means tests for each variable respectively.

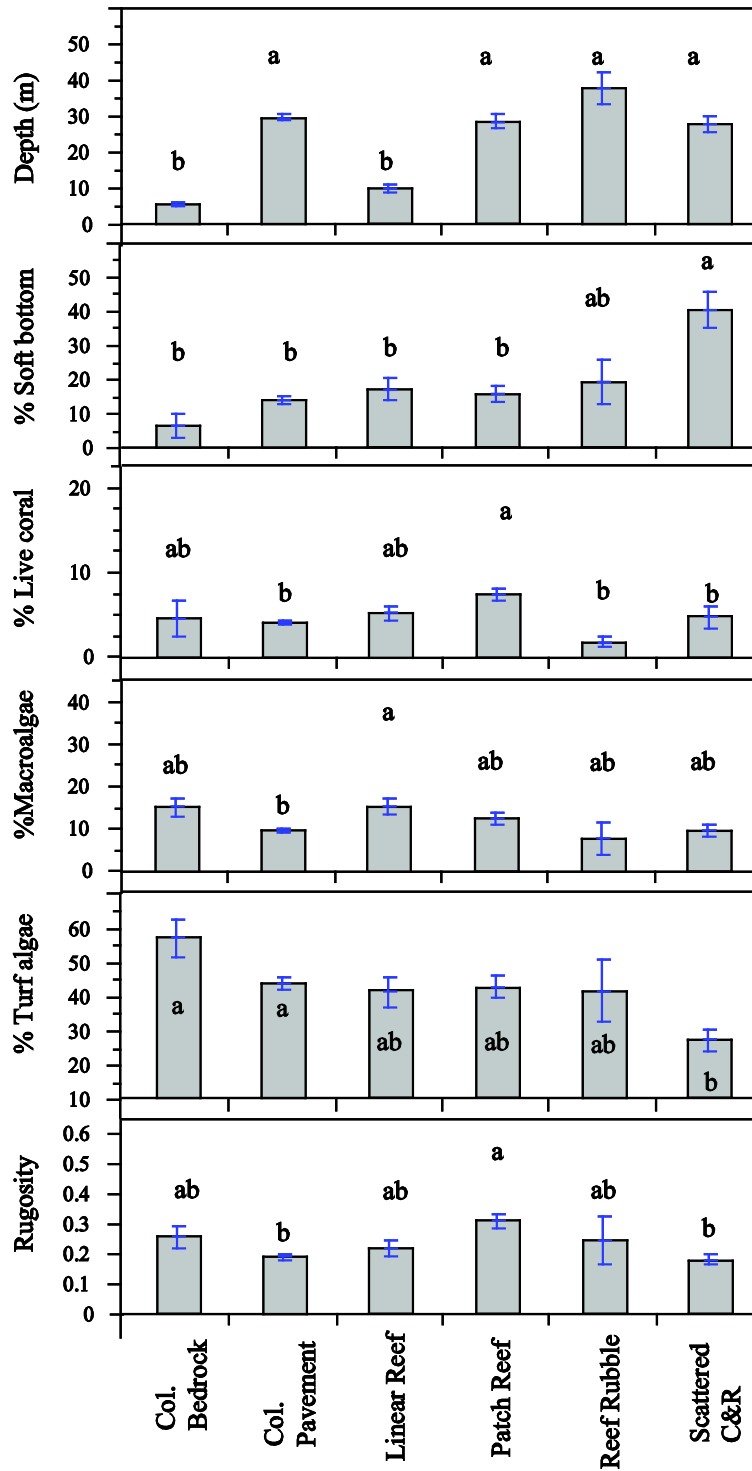


Figure 3.7: Mean (\pm SEM) for **local environmental characteristics** within reef types identified by **low resolution** mapping. Letters denote reef types that showed no significant differences among means for each variable respectively.

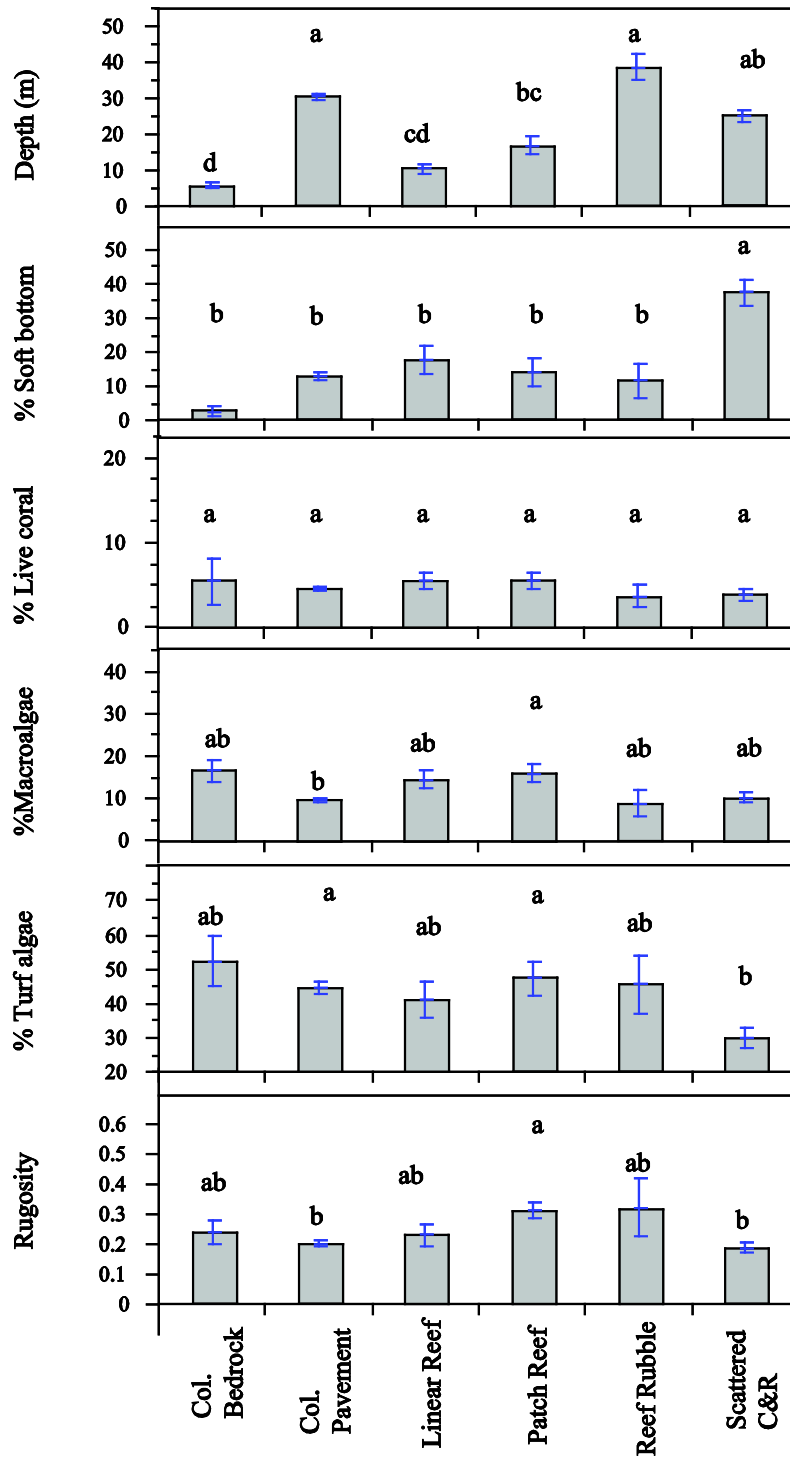


Figure 3.8: Mean (\pm SEM) for **local environmental characteristics** within reef types identified by **high resolution** mapping. Letters denote reef types that showed no significant differences among means for each variable respectively.

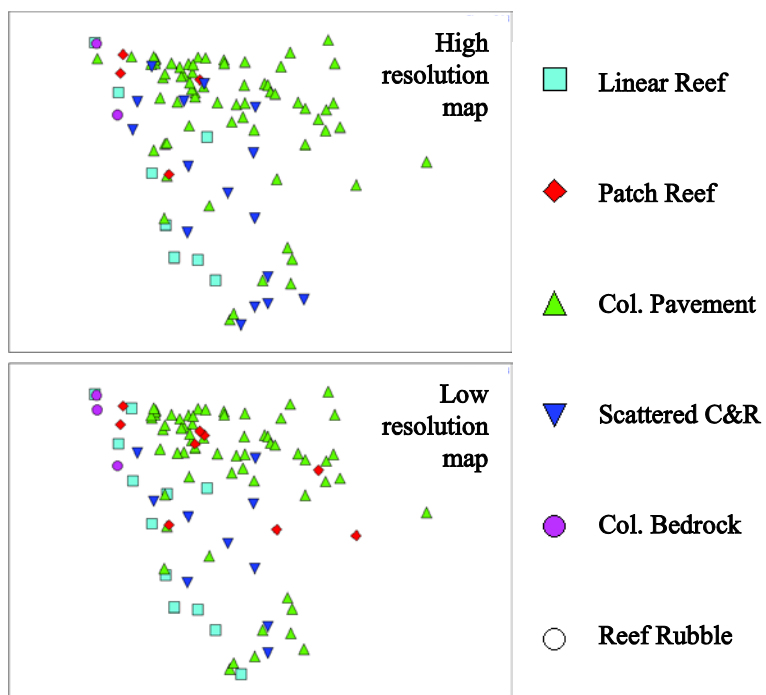


Figure 3.9: MDS of sites by **local habitat characteristics** for one of the five randomly chosen subsets of the survey data (stress = 0.14). Sites are coded by reef type identified from benthic maps.

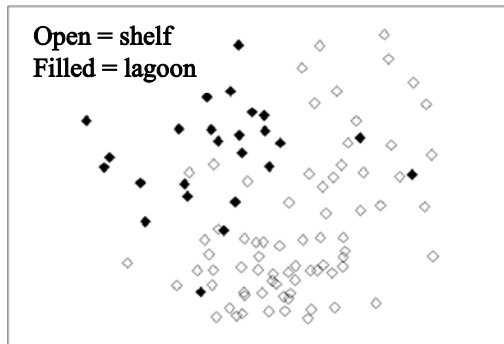


Figure 3.10: MDS of sites by **fish communities** for one of the five randomly chosen subsets of the survey data (stress = 0.22). Sites are coded by geomorphological zone identified from benthic maps.

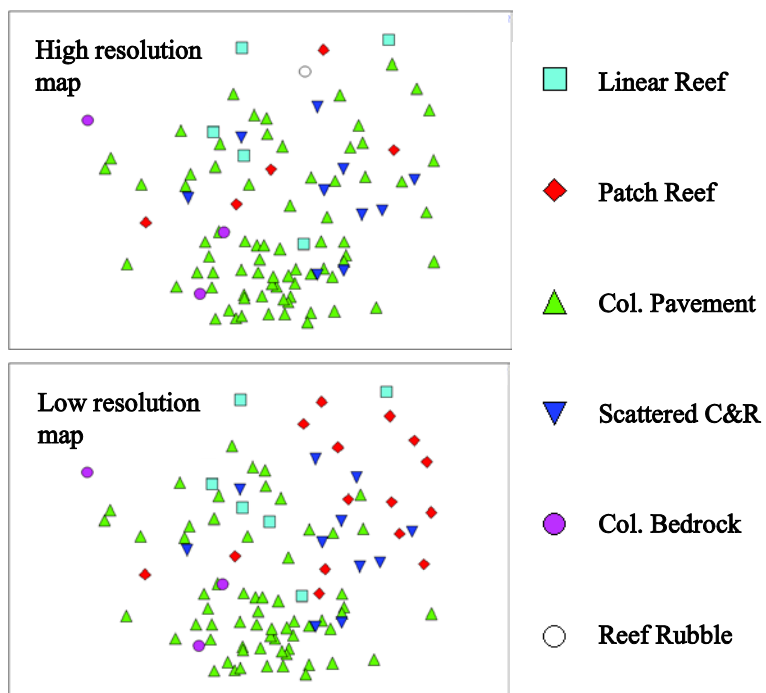


Figure 3.11: MDS of sites by **fish communities** for one of the five randomly chosen subsets of the survey data (stress = 0.22). Sites are coded by reef type identified from benthic maps.

Chapter 4: How big are fish scales?

Abstract

Correlations between fish assemblages and surrounding landscape variables were measured using univariate linear regression for a range of scales between 25 and 800 m. The strength of the associations as a function of scale could be grouped into 6 response curve forms and were used to identify the scale that best correlates fish with their surrounding habitat. Several dependent variables were used in the analysis including overall species richness and total fish abundance, species richness and abundance of fish in the mobility guilds transient, mobile, and resident, and the abundance of six common reef fish species respectively that were further separated into total, juvenile, and adult categories. The independent or landscape variables used were area of seagrass or submerged aquatic vegetation (SAV), length of hard bottom edge, area of sand or unconsolidated sediment, and habitat diversity. To evaluate the influence of map type, the landscape variables were calculated based on four separate benthic maps. Maps were produced using two levels of spatial and thematic resolution respectively. Individual landscape variables explained a maximum of only 25 % of the variability in fish distributions. Habitat diversity was a poor predictor of all aspects of the fish community. Seagrass/SAV and Sand/sediment area predicted distribution of many fish, not just those considered obligate users. Length of hard bottom edge was correlated with more of the fish variables than any other landscape feature tested. Landscape correlations for individual species achieved a wider range

and more extreme values than comparisons involving mobility guilds or the entire fish assemblage. Scales of peak correlation were the same for juveniles and adults in over half of the comparisons. Transient species exhibited broader scales of peak correlation than either resident or mobile fish in a large number of comparisons. Use of different input maps resulted in a changed perception of either the strength of peak correlation at a given scale, or the scale at which peak correlations occurred for many comparisons involving hard bottom edge length and area of sand. In contrast, results were quite consistent regardless of map type for comparisons involving seagrass/SAV area and habitat diversity. Detection and perception of fish-landscape correlations depend on the type of map that is used, the range of scales tested, and the interval or distance between analysis scales.

Introduction

Ecologists have long hypothesized that the abundance and distribution of fishes is partially determined by surrounding habitat types (e.g. Randall 1965, Ogden 1976, many others). Up to now, the availability of synoptic data with broad spatial coverage limited attempts to test these ideas. Recently, advances in Geographic Information System (GIS) software, satellites, and sonar mapping have resulted in a substantial increase in the availability of appropriate data such as maps of the benthos. As a result, several studies have now quantified the influence of surrounding landscape elements on the structure of local fish communities. For example, studies have shown that the distribution and abundance of several fish species, individual life stages, trophic guilds, mobility guilds, in addition to fish diversity on reefs can be

influenced by landscape factors such as the areas of adjacent seagrass, soft bottom, and hard bottom in the vicinity (Kendall et al. 2003, Kendall et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007, Pittman et al. 2007, Drew and Eggleston 2007).

The studies cited above relied on benthic maps as a source of independent variables with which to establish relationships between fish and their surrounding habitat. Benthic maps are, however, abstract representations of actual bottom features and have particular spatial and thematic characteristics as a result of the processes and source data that were used to produce them (Andréfouët et al. 2003, Kendall and Miller 2008, Prada et al. 2008). Spatial characteristics may include the size, shape, and edge length of features represented in the maps. Thematic characteristics may include the number and variety of categories with which the bottom features are described. Each of the early studies relied on an individual map and its particular spatial and thematic resolution. However, it is known that spatial and thematic decisions made during map production can profoundly affect map characteristics (Andréfouët et al. 2003, Kendall and Miller 2008). For example, spatial and thematic resolution can dramatically influence the characteristics of maps of terrestrial landscapes (e.g. Turner et al. 1989, Benson and MacKenzie 1995, Saura 2002). For coral reef ecosystems, Andréfouët et al. (2003) found that map-based quantitative descriptions of coral atolls differed by as much as 28% depending on the spatial resolution of satellite data used to produce them. Similarly, Kendall and Miller (2008) found that the depiction of many features of reef ecosystems was sensitive to changes in both spatial and thematic resolution of the maps characterizing them. In their study, increasing thematic resolution greatly increased the number of map

polygons, total edge length of polygons, and the diversity of maps, whereas changing the spatial resolution resulted in disproportionate changes in the area, perimeter, and other values among bottom types. Additionally, Kendall and Miller (2008) reported that estimates of the number of features, average feature size, and total edge spanned an order of magnitude among maps that differed in thematic and spatial resolution. Given the influence of spatial and thematic map resolution on the quantification of landscapes, I hypothesized that relationships between reef fish and benthic habitats derived from such maps would be sensitive to their spatial and thematic resolution. Indeed, map differences will almost certainly have an influence on the type of inferences and sensitivity of landscape ecological studies to detect and measure landscape influences on fish distribution and abundance.

Map characteristics associated with different levels of thematic and spatial resolution may influence the results of ecological studies in several ways. For example, the amount of the habitat deemed essential to a particular species or community that appears in maps can differ depending on the spatial and thematic resolution used in map production. Small habitat patches or highly specific bottom types can be lumped in with larger features or similar bottom types as spatial and thematic resolution are reduced. Many species specialize on use of edges or ecotones between habitats (Shulman 1985, Sweatman and Robertson 1994, Dorenbosch et al. 2005, Vanderklift et al. 2007, Pittman et al. 2007, Valentine et al. 2007). Such habitat boundaries can be greatly simplified or even removed depending on map characteristics (Kendall and Miller 2008). It might be expected that the real landscape that fish communities interact with and are influenced by are most accurately depicted

by maps with very high spatial and thematic resolution. Thus, use of high resolution maps could be expected to yield the strongest correlations between fish and their landscapes. Additionally, such maps would also yield the lowest correlations, relative to other map types, when no association is present. Highly-detailed maps are, however, very expensive and time consuming to produce. As maps are generalized into coarser thematic and spatial depictions of the landscape, they are cheaper and faster to produce, but these changes have unknown consequences on our ability to detect correlations among fish community and landscape variables. Are highly detailed, highly resolved maps necessary for ecological analyses of fish?

Landscapes can affect the ecology of fish at several levels of organization. At the broadest level, aspects of the entire fish assemblage such as species diversity (richness and evenness) or total abundance of fish may be measurably related to landscape variables despite the diverse habitat requirements of the individual species included in the assemblage (e.g. Kendall 2005, Grober-Dunsmore et al. 2007, Pittman et al. 2007). At lower levels of organization, fish guilds, defined according to trophic or mobility roles and therefore with similar habitat or space requirements, may have greater correlation with landscape elements when considered separately from the rest of the fish assemblage (e.g. Grober-Dunsmore et al. 2007). Individual species would be expected to have even closer and more easily detectable relationships with landscape features (e.g. Grober-Dunsmore et al. 2007) without the added variability from multiple species that utilize slightly different niche spaces and habitat features. The very highest level of correlation between fish and their landscapes might be expected for individual life stages of particular species because all such fish utilize

the same discrete spatial scale and habitat types (e.g. Kendall et al. 2003, Grober-Dunsmore et al. 2007). This is likely true even for fish species considered to be habitat generalists. Fish-landscape correlations based on single life stages would eliminate the added variability resulting from the different scales of landscape utilization associated with lumping juvenile and adult stages together.

The strength of correlations between fish and their landscapes are likely scale-dependent and based on fish size, mobility, taxonomy, life stage, and habitat requirements (Kramer and Chapman 1999, Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007). Body size in fish has been positively correlated to home range size among (Kramer and Chapman 1999) and within species (Overholtzer and Motta 1999). Similarly, juveniles of a given species, by virtue of their relatively smaller size, could be expected to interact with adjacent landscape features at shorter distances than adults (Grober-Dunsmore et al. 2007). The abundance of those species that utilize a single rock, coral head, or burrow for most of their life history, termed resident species, would be expected to exhibit correlations only with habitat measures for their immediate vicinity. Fish in the genus *Stegastes* defend territories of 1-5 m² for food and breeding purposes and provide a good example of resident species (Itzkowitz 1977, Luckhurst and Luckhurst 1978). Those species that range more widely using larger habitat patches or perhaps even a variety of habitat types, termed mobile species, would not be expected to be correlated with the just the habitats in the immediately vicinity of where they were caught: rather mobile species would be expected to have measurable correlations with landscape features at distances of 10's to 100's of meters away depending on their home range size (Kramer and Chapman

1999). Examples of such species include haemulids (Burke 1995, Tulevich and Ricksiek 1994), acanthurids (Morgan and Kramer 2004), and scarids (Chapman and Kramer 2000, Mumby and Wabnitz 2002). Finally, those species that range widely across the landscape, termed transient species, would be expected to have correlations with landscape elements at even greater distances. Such species include many fish in the family carangidae and lutjanidae species such as *Ocyurus chrysurus* (Chapman and Kramer 2000).

The scale of fish-landscape interactions can be identified by evaluating a local fish assemblage in the context of its position relative to adjacent elements in the benthic landscape (Irlandi and Crawford 1997, Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007, Vanderklift et al. 2007). However, the spatial extent of elements to include in any analysis is critical. If too small a spatial scale is used, weak correlations will be found between the landscape and local fish assemblage because landscape elements used by the taxa considered are not included in the analysis (left hand portion of Figure 4.1a). Conversely, if the analysis is conducted at too broad of a spatial scale, weak correlations will again be found, but this time because too many landscape elements not used by the taxa under consideration are being included (right hand portion of Figure 4.1a). Presumably, correlations will be maximal at an intermediate scale (Figure 4.1a). Thus, analyses should seek to systematically vary the spatial scale and distances over which fish and landscape associations are measured (Addicot et al. 1987, Wiens et al. 1987, Wiens 1989, Riitters et al. 1997, Sale 1998, Kendall 2005). Once correlations between a fish assemblage and parameters for the adjacent landscape have been established across a

range of scales, the strength of the associations can be examined to find the scale that best correlates fish with their surrounding habitat. Use of this “best” scale approach to empirically define the ecological scale has recently emerged in a handful of terrestrial (Pearson 1993, Karl et al. 2000, Ricketts et al. 2001, Steffan-Dewenter 2003, Holland et al. 2004, Holland et al. 2005) and marine studies (Kendall 2005, Grober-Dunsmore et al. 2007).

Plots of correlation strength and analysis distance are not constrained to appear as demonstrated in Figure 4.1a. Previous terrestrial (Pearson 1993, Karl et al. 2000, Ricketts et al. 2001, Steffan-Dewenter 2003, Holland et al. 2004, Holland et al. 2005) and marine studies (Kendall 2005, Grober-Dunsmore et al. 2007) using this approach have yielded several distinct patterns (Figures 4.1a-f). As discussed above, a clear peak in correlation strength may occur at a discrete scale (Figure 4.1a). This would be expected for organisms with a clear association with the landscape variables in question and a well defined home range of intermediate size relative to the scales evaluated. The next functional form that has been found is a completely flat response wherein the strength of correlation is uniform across all analysis scales (Figure 4.1b). This could simply occur because the organism is not correlated with the landscape variable at any scale (Figure 4.1b, lower line) or when correlation is present but at the same level across a range of scales (Figure 4.1b, upper line). This latter situation could arise when an organism utilizes a habitat resource with equal efficiency at a variety of distances. A further possible pattern is one of a monotonic response with analysis scale, either positive (Figure 4.1c, d) or negative (Figure 4.1d, e). Steadily increasing correlations (Figure 4.1c) with scale indicate an organism with large home

range, the maximum size of which has not been reached in the range of scales tested. Steeply rising then flattening curves (Figure 4.1d) could be found for organisms with a moderate to large home range size (but not small). Steadily declining correlations (Figure 4.1e) are likely for species with small to moderately sized home range. Initially high then rapidly declining correlation (Figure 4.1f) would be expected for organisms with small home range size and are not even indirectly influenced by the tested landscape resource more than a short distance away. It is unknown if input maps with different spatial and thematic properties will result in identification of consistent patterns and scales of correlation between organisms and landscape variables.

Ideally, the scale and strength of correlation between the fish assemblage and landscape would be the same for maps of any spatial and thematic resolution. However, this need not be the case. Most simply, map type may alter the strength of the correlation but not the scale at which it is maximal. This is not a serious problem if the objective is to merely identify the scale of peak correlation but is of concern if the goal is accurate measurement of the actual intensity of the correlation. Of greater concern are circumstances in which the map type affects both the scale and magnitude of the correlation. In this case the highest correlation between a fish assemblage and landscape variable would be found at entirely different scales depending on the type of map used in the study. Such an event calls for the most careful consideration of the consequences of relying on a particular map type.

The central question I ask here is “How much of the pattern in fish distribution can be explained using landscape variables?” Prior terrestrial studies of

the relationship between landscape variables and biological indices explained 2 to 64% of the variability in bird guilds (Pearman 2002), bee and wasp species richness (Steffan-Dewenter 2003), beetle abundance (Holland et al. 2004), and moth species richness (Ricketts et al. 2001). Although less studied, findings from multiscale studies of reef fish have found a similarly wide range with between 11 and 94% of the variability explained between landscape variables and fish species richness (Kendall 2005) and other fish community measures (Grober-Dunsmore et al. 2007). Here, I seek to quantify the influence of spatial and thematic resolution on inferences regarding the role of landscape patterns in influencing biological distributions of fish. In so doing, I seek to test the following specific hypotheses generated by the issues raised above.

- 1) Distribution of reef fish will be correlated with landscape variables such as area of sand or seagrass, length of hard bottom edge, and habitat diversity,
- 2) Strength of the correlation between fish distribution and landscape variable will vary with the spatial scale of the analysis,
- 3) Strength of correlations between fish and landscape variables will have one of six characteristic forms when plotted against analysis scale (Figure 4.1 a-f),
- 4) Thematic and spatial resolution of maps will affect the strength and spatial pattern of the correlation between fish and their landscapes,
- 5) Maps with highest spatial and thematic resolution will yield the highest correlations between fish assemblage and landscape variables,

6) Relationships between fish and their landscapes will have highest correlation for individual life stages of species followed by guilds and lowest for whole community metrics,

7) Resident fish species will have highest correlation with landscape variables at shorter distances than mobile, followed by transient species, and

8) Juveniles of a given species will have highest correlation with landscape variables at shorter distances than adults.

Methods

This study was based on the marine landscape and fish communities around Buck Island Reef National Monument (BIRNM), US Virgin Islands (Figure 4.2). Sampling design around BIRNM was devised to address NPS monitoring needs inside versus outside of park boundaries. The monitoring design has resulted in independent sample sites spread widely in the study area with each surrounded by a unique combination of habitat elements. The present study utilized this diversity of landscape conditions around hundreds of independent samples to identify relationships between the distribution of fish and their local and surrounding bottom types. The area has been intensively mapped and characterized for National Park Service (NPS) monitoring. Fish census data was used to create dependent variables and four types of benthic maps were used to calculate landscape or independent variables around each fish survey site.

Fish Survey Data

Visual surveys have been used to census the fish and bottom features within and around BIRNM. Sampling was conducted according to a stratified random design with sites distributed in hard versus soft bottom and among management zones. Only hard bottom surveys were used in the present analysis. Between January 2002 and May 2006, 588 sites were surveyed. At each of these sites, a diver swam along a randomly selected compass heading and recorded all fish observed within a 25 by 4 meter belt transect (100 m^2) to the lowest possible taxon. Divers estimated fork length and recorded fish abundance within 5 cm size classes. Diver swimming speed was maintained to complete the survey in ~15 minutes regardless of substrate type or complexity.

A hierarchical approach was taken in selecting response variables to test hypotheses relating fish distribution at several organizational levels within the assemblage to landscape attributes (Table 4.1). First, measures of the entire fish assemblage, species richness and total fish abundance, were created for each survey site. These response variables were chosen because the number of species and number of fish present on reefs are thought to be influenced by surrounding landscape features (Kendall 2005, Grober-Dunsmore et al. 2007, Pittman et al. 2007). Next, the fish community was divided into mobility guilds for analysis. Mobility guilds, assigned at the species level, were transient (T), mobile (M), and resident (R) and are thought to relate to the distances over which species interact with their landscapes (Grober-Dunsmore et al. 2007). Species richness and fish abundance within each of the three guilds respectively were summarized as the response variable of each site.

Next, the abundances of six common reef fish species at each survey site were considered. The six species were chosen based on several criteria: 1) representation from diverse family and trophic groups, 2) known life history and local habitat preferences to aid in interpretation of any landscape-scale correlations, and 3) common occurrence in the study area to ensure relatively large sample size and enable robust analysis. Abundances of these species were also separated into juvenile and adult categories respectively for life stage-specific analysis. This hierarchical approach was taken to not only evaluate the individual landscape correlations within different organizational levels of the fish community, but also to test the hypothesis that individual life stages of particular species would have stronger correlations with landscape variables than whole community metrics.

Benthic Maps

Four benthic maps of the BIRNM area were produced using two levels of spatial and thematic resolution respectively (Kendall and Miller 2008). Maps were created from orthorectified aerial photographs and visual interpretation using GIS software (Kendall et al. 2001). A relatively large minimum mapping unit (MMU, size of the smallest feature to be mapped) of 4047 m² (1 acre) and a much smaller MMU of 100 m² (0.0247 acre) were used. A hierarchical classification scheme was used to attribute maps at both spatial scales. The scheme categorized bottom features into 17 subcategories nested within 3 main categories. The main categories were unconsolidated sediment, submerged vegetation, and hard bottom (Table 4.1). The original maps with 17 classes served as high thematic resolution maps. Subsequently, I dissolved the boundaries and aggregated the polygons of these high thematic

resolution maps to the 3 thematic class level for use in the analyses as maps with low thematic resolution. This process resulted in four maps of the same area using the same approach but with different spatial and thematic characteristics (Figure 4.3). These maps are representative of the typical range of thematic and spatial resolutions presently available to produce maps of reef ecosystems.

There are many potential landscape variables that can be calculated. We chose four that were representative of broad classes of landscape metrics: 1) area of seagrass or SAV, 2) length of hard bottom edge, 3) area of sand or unconsolidated sediment (map with high or low thematic resolution respectively), and 4) habitat diversity (Shannon Index). These measures were selected because of their suspected ecological significance as drivers of fish assemblage structure and distribution on reefs. The area of seagrass around reefs has long been suspected to enhance abundance of lutjanids (snappers), haemulids (grunts), and other fish on reefs (Randall 1965, Ogden 1976, Kendall et al. 2003, Kendall 2005, Grober-Dunsmore et al. 2007). Reef edges have been the focus of intensive research recently and are a key ecotone controlling structure in reef landscapes (Dorenbosch et al. 2005, Vanderklift et al. 2007), are favored hunting grounds for several species of fish (Shulman 1985, Sweatman and Robertson 1994, Valentine et al. 2007, Vanderklift et al. 2007), focus populations of some herbivorous fish (Wernberg et al. 2006), and must be transited by those species that use hard bottom as structural refuge but forage over soft bottom (Ogden 1976, Burke 1995) or among reef types. Sand and seagrass bottom plays an important role in providing settlement habitat for many reef fish species and may impact the number of recruits ultimately arriving on nearby reefs (Shulman and

Ogden 1987, Shulman 1985, Parrish 1989). Diversity of habitat types may be positively correlated with the diversity of the fish community (Ward et al. 1999) and has been suggested as a potential surrogate for overall diversity in selection of marine reserves (NRC 2001).

Multiscale Analysis

The dominant scales with which components of the fish assemblage are correlated with their local and surrounding habitat elements were identified using a multi-scale approach. The four landscape metrics were calculated around each of the 588 fish survey sites based on all four map types respectively. To determine which analysis scale “best” relates to a fish community variable, seascape metrics must be calculated for each fish census site at a range of distances (Figure 4.4). Measurement distances ranged from very small, including only seascape elements associated with the habitat directly at the fish census site, through broad scales that incorporated both the local habitat and the mosaic of habitat elements beyond the distance that fish were likely to be influenced. The smallest distance was 25 m to incorporate the entire area of each 4 by 25 m fish survey. Using a geometric progression, habitat metrics were also calculated at increasing distances of 50, 100, 200, 400, and 800 m radii around the starting point of each survey to include successively more of the surrounding habitat (Kendall 2005)(Figure 4.4). These landscape values served as independent variables in the regression analysis.

Univariate linear regression was used to determine the basic relationship between a given fish variable and the landscape variables at each scale. The strength of the relationship between the fish assemblage and landscape variables as a function

of spatial scale was evaluated using the Pearson correlation coefficient (r). This was chosen over other regression-based statistics, such as R^2 , to characterize relationships because it ranges from -1 to +1 and therefore both positive and negative relationships between variables can be perceived. The strength of the correlation between a given parameter of the fish community and a landscape parameter was calculated separately for each of the distances that landscape metrics were produced.

To avoid pseudoreplication, especially where larger analysis diameters (e.g. 800 m) would result in very similar landscape values around adjacent fish census sites, but maximize use of the data, a resampling approach was taken (Holland et al. 2004). In this technique, a non-overlapping subset of fish survey sites and their corresponding landscape values was randomly drawn from the entire pool of 588 data points. Preliminary analysis revealed that ~14 non-overlapping sites could be fit within the study extent when landscape variables were calculated at the largest radius of 800m. A univariate linear correlation was then performed on this subset of the data and the resultant r values were saved. These survey sites were then returned to the entire pool of data and another set of randomly selected points was extracted and used to calculate a second set of correlation statistics. If an identical set of 14 sites were selected by chance a second time, they were not included in the analysis. The data were resampled in this way until a stable set of correlation statistics was obtained (i.e. a unimodal set of r values with low standard error). Preliminary analysis revealed that 1000 iterations of the resampling procedure produced stable r values with very low standard error for all variables and analysis scales. This sampling process was conducted at all six analysis scales that landscape variables were calculated at (i.e. 25,

50, 100, 200, 400, and 800 m) for each combination of X and Y variables respectively. The mean and standard error of the 1000 r values from every scale were then plotted for each combination of X and Y variables. This enabled identification of the scale of maximum $|r|$ where the greatest correlation existed between each fish variable and landscape variable. These analyses were conducted using the software Focus v2.1 (Holland et al. 2004).

The resampling analysis was conducted for each of the four map types and the results for each fish and landscape variable were plotted on the same chart. This resulted in 104 individual plots (listed in Table 4.1, and provided in the Appendix). Each plot consists of a single fish and landscape variable and the average correlations between them measured at all six analysis scales based on each of the four map types. This was done to visualize the different correlations observed between fish and their landscapes when different map types were used to produce the landscape variables.

Hypothesis Testing

Four general outcomes were possible from our analyses. The simplest case was when no relationship was found between a given fish variable and landscape variable for any map type or analysis scale. Another possibility was that a significant correlation existed at one or more analysis scales and all map types yielded similar results. It was also possible that one or more analysis scales yielded a significant correlation, but the results were different depending on the map type used to create the landscape variables. This possibility could be subdivided into two outcomes: the maximum $|r|$ value among map types could occur at the same scale but achieve significantly different values or maximum $|r|$ values among map types could occur at

entirely different scales. The results of each of the 104 fish and landscape comparisons were tallied into one of these four categories using the rules defined below.

Hypothesis 1: The distribution of reef fish will be correlated with landscape variables such as area of sand or seagrass, length of hard bottom edge, and habitat diversity.

To evaluate the first of the four possible outcomes, the hypothesis that mean r values for each scale and map type were significantly non-zero was tested. It was found that with Bonferroni correction for testing 6 scales at once ($p < 0.008$ for significance), nearly all mean r values were significantly different than zero. This was due to the large number of resampling runs (1000) and resulting narrow SEM values. Even r values between +0.1 and -0.1, which would account for less than 1% of the variability in the relationship between the fish and landscape variables, were statistically significant. To infer ecological relevance, a much higher and more conservative $|r|$ of 0.2 was therefore selected as a cutoff for identifying more important relationships for further discussion. Such r values would account for 4% of the variability in the data and in all cases were significantly non-zero.

Hypothesis 2: The strength of the correlation between fish distribution and landscape variable will vary with the spatial scale of the analysis.

Only plots with at least one $|r|$ value > 0.2 for any scale or map type were considered further. For each plot, the scale with the highest $|r|$, regardless of map type, was identified as a focal scale for further analysis since this scale and map type

yielded the highest correlation between fish and landscape variables and could be used as a benchmark for comparing results with lower correlations.

We used a simple ANOVA to evaluate whether all 4 map types yielded a maximum r value ($|r| > 0.2$) at the same scale for a given fish and landscape variable combination. This tested the hypothesis that r values were significantly different among map types. This test was conducted for all four map types at the scale with the highest $|r|$ value. In cases where the ANOVA yielded a significant result, indicating that at least one r value among the four map types was different than the others, the third possibility described above was tested.

Hypothesis 3: The strength of correlations between fish and landscape variables will have one of six characteristic forms when plotted against analysis scale (Figure 4.1 a-f).

Correlation plots were examined for each combination of fish and landscape variable and each map type. Plots were qualitatively characterized according to the six possible correlation curves described by Figure 4.1 a-f.

Hypothesis 4: The thematic and spatial resolution of maps will affect the strength and spatial pattern of the correlation between fish and their landscapes.

To evaluate the possibility that peak r values occurred at the same scale but had significantly different values among map types with different spatial or thematic resolution, the scale with the highest r value was identified and the mean r -values among map types were tested for significant differences from each other using a Tukey-type multiple means comparison procedure. A more conservative $\alpha=0.001$ was

used to define significant differences due to the narrow SEM values that resulted from the resampling procedure.

To evaluate the possibility that peak r values occurred at different scales for different map types no additional statistical tests were needed. Simple peaks in $|r|$ values among map types at different scales from the map type with maximum $|r|$ are evidence of this outcome.

What were the relative frequencies of these possible outcomes? In particular, when input maps yielded different results, how often were peak $|r|$ values at the same scale but achieved significantly different values among map types? More importantly, how often did other map types have highest r values at completely different scales? Based on the map type and scale with the maximum $|r|$ value, the other three map types were evaluated. These two possible outcomes were tabulated within landscape variable categories for all comparisons in which at least one map type had a significant value ($|r| > 0.2$).

Hypothesis 5: Maps with highest spatial and thematic resolution will yield the highest correlations between fish assemblage and landscape variables.

To determine if there was a map type that consistently had the highest or lowest $|r|$ values for each of the four landscape variables investigated, comparisons with significant results were evaluated further. When a $|r| > 0.2$ was present and there was a significant difference among map types in r values, the map type with the highest and lowest $|r|$ values were recorded. The number of times each map type had the highest or lowest value was summarized in tabular format for each of the

landscape variables. Ties for highest or lowest values among two or more map types were not included.

Hypothesis 6: The relationships between fish and their landscapes will have highest correlation for individual life stages of species followed by guilds and lowest for whole community metrics.

Next, we evaluated the hypothesis that the highest correlations with landscape variables are found for individual life stages of particular species and lower values are found as multiple aspects of the fish assemblage are grouped together. To determine this, the maximum $|r|$ values for each of the 104 variable combinations were grouped and plotted by those that tested; 1) abundance of individual life stages (juvenile or adult) of particular species, 2) total abundance of particular species, 3) abundance or species richness of the mobility guilds, and 4) the whole assemblage variables of overall abundance or species richness. The $|r|$ values were separated by map type and landscape variables. The range and distribution of values were compared among levels of organization of the fish variables within in a given map type by rank ordering them and examining the highest and lowest values. These are the best measures of the diversity of correlation strengths among fish variables.

Hypothesis 7: Resident fish species will have highest correlation with landscape variables at shorter distances than mobile, followed by transient species, and

Hypothesis 8: Juveniles of a given species will have highest correlation with landscape variables at shorter distances than adults.

The hypothesis that juvenile fish have stronger correlations with landscape variables at finer scales than adults was also evaluated. The results were tallied for

each species, landscape variable, and map type. Habitat diversity was not evaluated because r values were very low across all scales and no clear peaks in correlation were observed. The scale of peak correlation between juveniles and a given landscape variable was identified for each map type and simply compared to the scale of peak correlation for adults. The distance of peak correlation of juveniles relative to adults was described as one of the following: juvenile < adult, adult < juvenile, or when the scale of peak correlation was the same for both of these life stages, juvenile = adult. In similar fashion, the hypothesis that resident fish have higher correlations with landscape variables at finer scales than mobile or transient fish, which should have highest correlations at successively broader scales, was evaluated.

Results

Hypothesis 1: The distribution of reef fish will be correlated with landscape variables such as area of sand or seagrass, length of hard bottom edge, and habitat diversity.

Correlations between fish and landscape variables were low overall (Appendix A). Of the 2496 mean r values calculated, only 220 (~11%) exceeded the selected significance level of $|r|=0.2$. The highest value observed in the study was $|r| = 0.5$ between the abundance of *Cephalopholis fulvus*, a small grouper and the amount of hard bottom edge. Habitat diversity was not correlated with any fish variable at any scale (Table 4.1). Generally, correlations between fish and landscape variables explained such a low percentage of the variability in fish distribution that an individual landscape variable could not be expected to predict fish distributions.

Despite the lack of strong correlations between individual landscape variables and fish distributions, some relationships between fish and specific landscape variables were found. Area of seagrass/SAV was correlated with total species richness, species richness of resident fish, and abundance of at least one life stage of all species considered except for *Acanthurus coeruleus* (Table 4.1). The highest $|r|$ values found with seagrass/SAV were for *Stegastes planifrons* juvenile and total abundance, and *Cephalopholis fulvus* juvenile, adult, and total abundance (negative correlations). Species richness and abundance of transients, abundance of residents, and overall species richness all had positive correlations with area of sand/sediment (Table 4.1). Length of hard bottom edge was correlated with more of the fish variables (17) than any other landscape feature (Table 4.1). Species richness, resident species richness, mobile species richness, and abundance of all species except for *Ocyurus chrysurus* were related to length of hard bottom edge. Highest $|r|$ values found with hard bottom edge length were for *A. coeruleus* adult and total abundance, *C. fulvus* adult and total abundance (negative correlations), and *Sparisoma viride* juvenile and total abundance.

Hypothesis 2: The strength of the correlation between fish distribution and landscape variable will vary with the spatial scale of the analysis.

This hypothesis was true for all comparisons with significant r values although the results differed by landscape variable. Most peak correlations involving area of seagrass/SAV were found at the broadest scale considered of 800 m. As might be expected from the definition of the guilds, transient guild richness, and transient

guild abundance had highest correlation at 800 m with sand/sediment area. In contrast resident guild abundance had highest correlation at 25 m for the same landscape variable.

Patterns for correlations between individual species and landscape variables were less predictable. The abundance of adult *Cephalopholis fulvus* had highest correlation with sand/sediment area at 100 m whereas overall and juvenile abundance had highest correlation at 25 m. Most peak correlations with length of hard bottom edge occurred at the broadest scale considered (800 m) except for total and adult abundance of *Haemulon flavolineatum* and species richness of mobile species which occurred at 50 m. All peak $|r|$ values showed positive relationships except for *C. fulvus* which showed negative r values which were among the lowest observed in the study.

Hypothesis 3: The strength of correlations between fish and landscape variables will have one of six characteristic forms when plotted against analysis scale (Figure 4.1 a-f).

When strength of correlation is plotted against analysis scale several distinct shapes emerged (Appendix A). The simplest of which was when no change in correlation occurred among scales. This was observed for nearly all comparisons involving habitat diversity (e.g. Figure 4.5) because correlations were generally low across all analysis scales. Also observed frequently were cases in which the correlation steadily rose with increasing analysis scale. This was observed in many of the comparisons involving area of seagrass/SAV (e.g. Figure 4.6). Asymptotic curves were observed for many comparisons as well wherein correlations were low at short

analysis distances then rapidly rose and leveled off at broader analysis distances (e.g. Figure 4.7). This pattern was especially evident in comparisons involving hard bottom edge and maps with the highest spatial and thematic resolution (e.g. Figure 4.8). Maps with less spatial and thematic detail in the same comparison rose to the same maximum correlation at 800 m but did so more slowly and steadily. Less commonly observed were rapidly or steadily declining correlations as analysis scale increased which only occurred in comparisons involving sand/sediment and maps with high thematic resolution (e.g. Figure 4.9).

Hypothesis 4: The thematic and spatial resolution of maps will affect the strength and spatial pattern of the correlation between fish and their landscapes.

Support for this hypothesis was equivocal. For some of the landscape variables, spatial and thematic resolution influenced results, for others they did not. For comparisons involving habitat diversity, all four map types yielded similar results with $|r|$ values rarely exceeding 0.1 across all scales. For seagrass/SAV area, the scale of highest correlation was the same for all four map types in all but 1 of the 14 comparisons with significant results (i.e. $|r| > 0.2$). The exception was for abundance of juvenile *Ocyurus chrysurus* which had highest r at 800 m for the map with low spatial and thematic resolution, whereas the other map types yielded significantly lower mean r values at 800 m and instead had peak values at 400 m (Figure 4.7). Despite these measurable differences in *O. chrysurus* correlation, the total range in r values among maps of different thematic and spatial resolution at these scales was only ~ 0.05 , hence it is unlikely these differences are ecologically significant. Unlike those

for area of seagrass/SAV, all sand/sediment area results were strongly influenced by map type. Maps of the same spatial resolution resulted in similar r values at all spatial scales, whereas maps with differing spatial resolution resulted in very different values across scales (e.g. Figure 4.9). More specifically, the abundance of adult *Cephalopholis fulvus* had highest correlation with sand/sediment area at 100 m whereas overall and juvenile abundance had highest correlation at 25 m. However, these were perceived as positive relationships only when maps with low thematic resolution were used. For length of hard bottom edge, map type significantly influenced the results for all but 1 of the 17 comparisons with at least one $|r| > 0.2$. Only species richness of residents was consistently correlated with hard bottom edge by all four map types (Figure 4.8). For the 16 other comparisons, use of different map types resulted in either significantly lower r at the same scale or even a peak in r at an entirely different scale.

Table 4.2 presents the pattern of responses in the spatial scale of maximum correlation. Changes in map type had no effect on the spatial scale of maximum correlation for habitat diversity comparisons. When map type had an effect on the sand/sediment results, maximum $|r|$ value, peaks occurred at completely different scales rather than simply peaking at the same scale but at a significantly lower value. In contrast, seagrass/sav and hard bottom edge relationships showed some of each type of difference. Overall, the two types of differences (i.e. peak at different scale versus peak at the same scale but different strength) occurred with approximately equal frequency.

Hypothesis 5: Maps with highest spatial and thematic resolution will yield the highest correlations between fish assemblage and landscape variables.

The number of times that a map type had the highest or lowest $|r|$ value when a significant value was present (i.e. $|r| > 0.2$) was tallied in tables 4.3a-b. Only hard bottom edge comparisons yielded a consistent pattern. Maps with high spatial and thematic resolution had significantly highest $|r|$ values in 5 of the 17 comparisons with significant results. Maps with low spatial and thematic resolution also had significantly lowest $|r|$ values in 5 of the 17 comparisons.

Hypothesis 6: The relationships between fish and their landscapes will have highest correlation for individual life stages of species followed by guilds and lowest for whole community metrics.

Maximum $|r|$ values showed similar minima, maxima, and ranges among individual life stages of the 6 focal species and when all life stages were grouped together. Values for mobility guilds and whole fish community results were also similar to each other but quite different from those based on individual species (Figures 4.10a-d). Findings were therefore grouped into these two broader categories respectively. Of the 104 fish and landscape combinations tested, at least 11 of the highest max $|r|$ values were for species level analyses. This was true for all map types except for high spatial and low thematic resolution which had only 4 of the highest values (Figure 4.10d). Species level analyses also had a higher range of values (~ 0.4), much higher than the range for guild or community comparisons (~ 0.2) (Figures 4.10a-c). The exception was again for analyses based on maps with high spatial and

low thematic resolution which differed from this pattern in that the range of values was lower (~ 0.3) (Figure 4.10d). Also of note, nearly all of the highest $|r|$ values were for comparisons involving the landscape variables hard bottom edge length and seagrass/SAV. Nearly all of the lowest values were for correlations between habitat diversity and individual species.

Hypothesis 7: Resident fish species will have highest correlation with landscape variables at shorter distances than mobile, followed by transient species, and

Overall, 38% (9 of 24) of the comparisons had maximum correlations at the same scale for resident, mobile, and transient species (Table 4.4). The next most common result occurred in 30% (7 of 24) of the comparisons and was when transient species had larger scale of correlation than either resident or mobile species (which had a common scale of peak correlation). The expected result of r value trends being resident < mobile < transient occurred in only 1 of the 24 comparisons evaluated. Also of note, no landscape and fish variable correlations based on mobility yielded the same results for all four map types and differences were unpredictable and inconsistent.

Hypothesis 8: Juveniles of a given species will have highest correlation with landscape variables at shorter distances than adults.

Overall, 56% (40 of the 72) of the comparisons evaluated had maximum correlation at the same scale for both adults and juveniles of a given species (Table 4.5). Juveniles had a finer scale of peak correlation in only 15% (11 of 72) of the

comparisons, whereas adults had finer scales of peak correlation in 30% (21 of 72) of the comparisons. Of note, when a difference was found in comparisons involving seagrass/SAV, it was always that adults had finer scale of peak correlation than juveniles. All four map types generally resulted in the same patterns. Exceptions to this were for *Ocyurus chrysurus* and *Cephalopholis fulvus*. For *O. chrysurus*, use of maps with high spatial resolution resulted in juveniles having finer scales of peak correlation than adults. When low spatial resolution was used, the inverse pattern was perceived. For *C. fulvus*, use of maps with high spatial resolution resulted in adults having finer scales of peak correlation than juveniles. When low spatial resolution was used, the inverse pattern was perceived.

Discussion

The landscape metrics selected for study were thought to be among those with the greatest explanatory power over fish distributions. Despite this, the present results suggest that, alone, landscape variables can be expected to explain only a relatively small amount of the variability in the abundance and distribution of fish in coral reef systems. Overall, the observed correlations among fish measures and landscape variables were quite low, never explaining more than 25 % of the variation in the data. By themselves, univariate models appear insufficient to predict fish distributions and therefore advise spatially-explicit management of reef ecosystems.

The low correlations found in this study should not have been entirely unexpected. Findings from studies using a similar multiscale approach in terrestrial systems have generally yielded a similar range of correlation values to those reported here. Simple regressions of species richness of bird guilds and forest cover at

different spatial scales exhibited peak values of $r = \sim 0.16$ to 0.49 (Pearman 2002). Similarly, correlations among bee and wasp species richness with habitat diversity at different spatial scales had maximum r values of only ~ 0.2 to 0.4 (Steffan-Dewenter 2003). Further, linear correlation between beetle abundance and forest cover had maximum $|r|$ values of ~ 0.2 to 0.3 for each of 12 species tested (Holland et al. 2004). However, in some instances, stronger predictive power was found. Linear correlations between moth species richness and nearby forest area reached values as high as $r = \sim 0.7$ to 0.8 (Ricketts et al. 2001). Findings from other multiscale studies of reef fish have found a wider range in strength of correlation than those found here. Linear correlation between fish species richness on sand sites with area of nearby hard bottom reached maximum values of $r = 0.33$ in a separate study at BIRNM (Kendall 2005). Grober-Dunsmore et al. (2007) reported linear correlations between reef fish community variables and area of seagrass as high as 0.97 and were often in the range of ~ 0.5 to 0.6 in a recent study around the nearby island of St. John, US Virgin Islands. These results might suggest that landscape variables do afford the ability to predict fish distributions. I suggest this implication is unwarranted, as I believe the reported correlations likely results from the narrower range of types of sites in that study. Grober-Dunsmore et al. (2007) selected sites specifically to quantify the effects of variation in the amount of nearby seagrass cover. As such, results may have inflated the strength of the relationship relative to a randomly selected set of reefs. In addition, variation in other factors that could influence fish communities such as coral cover, rugosity, depth, distance from shore, and other variables was minimized during site selection (Grober-Dunsmore et al. 2007). While

this enhances the ability to detect an influence on fish communities due to seagrass by limiting the variability from other sources, which was the objective of that study, doing so limits the scope of inference of the findings to only the specific type of reef selected. Because the present study utilizes randomly selected sites from all of the hard bottom in the study area, the scope of inference is maximized and I believe provides a more comprehensive, ecosystem wide, measure of the strength of the relationship. While the correlations measured in the present study are lower, they are representative of effects for all of the hard bottom in the study area not just a subset of chosen reefs or reef types.

What landscape variables had the highest or most correlations with the fish variables? Habitat diversity has been considered as a proxy for fish diversity in the selection of marine reserves (NRC 2001). However, my results suggest that habitat diversity is a very poor predictor of species richness or indeed any component of the fish community considered in this study. This was surprising since a diverse landscape could be expected to translate into a rich species assemblage by affording a variety of niche spaces. Even at the finest scale, which encompassed all the habitat (s) within the 25 m fish survey, no correlations between habitat diversity and species richness were found. A possible explanation for this is that the benthic maps may not capture the aspects of habitat diversity to which fish respond. It is also possible that, although we evaluated a wide range of variables representing the fish assemblage, the species and assemblages considered may be habitat generalists or have considerable plasticity in requirements for a particular habitat type. My results add to a growing body of evidence against using habitat diversity at the landscape scale, as depicted in

benthic maps, as a proxy for overall fish and biotic diversity in selection of marine reserves (Donaldson 2002, Grober-Dunsmore et al. 2008, Pittman et al. 2007).

Area of seagrass/SAV was correlated with several of the fish community variables including at least one life stage of most of the species tested. This confirms the results of prior studies on species suspected to be influenced by this bottom type and further quantifies those relationships (Kendall 2005, Dorenbosch et al. 2005, Dorenbosch et al. 2006, Grober-Dunsmore et al. 2007, Valentine et al. 2007). Also found were correlations among fish distribution and SAV for many species not previously thought to be related to area of seagrass (e.g. *Cephalopholis fulvus*, *Sparisoma viride*, and *Stegastes planifrons*). This demonstrates the importance of seagrass/SAV as an influence on abundance and distribution of species on reefs generally, not just those considered obligate users. It also indicates that within a given landscape variable that a variety of direct and indirect mechanisms can operate that influence abundance of particular species or guilds. Sand/sediment area predicted several of the fish variables although not as many as expected given this bottom types role in settlement and foraging of many species. Length of hard bottom edge was correlated with more of the fish variables than any other landscape feature tested. This underscores its role as an important habitat margin to a diversity of fish in reef ecosystems (Dorenbosch et al. 2005, 2006, Valentine et al. 2007). Edges between reef types and soft bottom areas are often marked by abrupt changes in bathymetry that offer structural refuge supporting a diversity of reef species in high abundance (Pittman et al. 2007).

Correlations were found between diverse elements of the fish community and landscape features at a wide range of distances. Systematically changing the size of the analysis window and comparing fit among the models allowed the neighborhood that explains the highest amount of variability (highest $|r|$) in the fish data to be identified. The distance or neighborhood with the strongest correlation has been interpreted as the most ecologically influential or relevant scale for each combination of organism and landscape variable (Holland et al. 2004, Kendall 2005). My results indicate that this relationship can take on a wide range of functional forms. For many comparisons no significant relationships were found for any fish variables at any scale. In these instances, a number of factors may be responsible. The fish species, guilds, and community variables may be more closely related to a landscape variable not tested in this study. It could also be that the landscape maps used as input did not adequately capture the necessary detail of the landscape parameters that were tested. Fish may be distributed mostly or entirely in response to fine scale habitat features not detectable through remote sensing. Fish may even be responding to scales and landscape features beyond 800 m (our maximum analysis distance) from the site at which they were observed.

Ecologically-meaningful explanations are present for many of the observed patterns in neighborhood distance and associations with particular landscape variables. Species richness of fish was positively correlated with area of sand/sediment, area of seagrass/SAV, and length of hard bottom edge. Correlation with these variables increased with analysis distance such that maximum r values occurred at the 800 m scale, a broader scale of peak correlation than identified by

prior research (400 m by Kendall 2005, 500m by Grober-Dunsmore et al. 2007). It has long been believed that the area of surrounding seagrass increases the number of fish species on hard bottom sites by providing foraging areas for some species (Randall 1965, Ogden 1976, Nagelkerken et al. 2000), transfer of energy to reefs (Meyer et al. 1983, Meyer and Shultz 1985), nursery habitat (Dorenbosch et al. 2004, Adams et al. 2006, Dorenbosch et al. 2007, Verweij et al. 2008), and enhanced recruitment (Shulman and Ogden 1987, Cocheret de la Morinière et al. 2002). Similarly, area of surrounding sand bottom may result in enhanced recruitment to nearby hard bottom sites of the many species that initially settle in sand habitat to avoid reef and reef edge predators (Helfman et al. 1982, Shulman 1985, Shulman and Ogden 1987). Species richness on hard bottom sites may be enhanced by length of hard bottom edge through several mechanisms. Hard bottom edge must be transited for juvenile fish undergoing ontogenetic shifts following settlement in sand or seagrass (Shulman 1985, Shulman and Ogden 1987, Cocheret de la Morinière et al. 2002), it is a preferred hunting ground of some piscivores (Helfman et al. 1982, Quinn and Ogden 1984, Sweatman and Robertson 1994), and is the optimum location to seek structural refuge to minimize travel distance from reef to softbottom for species that undergo such daily foraging migrations (Kendall et al. 2003). Hard bottom edge around a site represents a key ecotone habitat for many species (Wernberg et al. 2006, Valentine et al. 2007, Vanderklift et al. 2007), and also indicates the presence of bathymetric complexity between reef types or reef and soft bottom which has been positively correlated with species richness of fish (Luckhurst and Luckhurst 1978, Gratwicke and Speight 2005ab, Pittman et al. 2007).

Ecologically-meaningful correlations were also found between individual species and certain landscape variables. Many of the described relationships were intuitive. For example, among the strongest negative correlations in the study were observed between *Cephalopholis fulvus* and length of hard bottom edge and area of seagrass/SAV. In both cases r values steadily decreased with analysis distance to a maximum at the 800 m scale for all life stages. This species utilizes flat hard bottom often sparsely colonized by corals, sponges, and gorgonians (pers. obs., unpublished data), a bottom type often described as pavement that typically covers broad areas (Kendall et al. 2004). Hard bottom edges or a large area of seagrass nearby would mean that there is less of their preferred flat hard bottom habitat. Logical ecological correlations were also observed between landscape variables and *Haemulon flavolineatum* adult and overall abundance. This species feeds solitarily over seagrass and softbottom at night but schools over reefs and hard bottom during the day (Randall 1965, Ogden 1976). Area of seagrass positively influenced abundance on reef sites by providing a large foraging area (Burke 1995, Nagelkerken et al. 2000, Kendall et al. 2003) especially at long analysis distances that may correspond to a broad foraging range (e.g. Figure 4.11). High correlation with hard bottom edge, especially at very short analysis distances, makes sense too since optimality theory predicts that *H. flavolineatum* will utilize reef sites near reef edges (Kendall et al. 2003). Such proximity minimizes energy costs and daily travel time from resting sites on reefs to adjacent seagrass foraging areas. This relationship was apparent only when maps with high spatial and thematic resolution were used (e.g. Figure 4.12).

More difficult to explain were the strong correlations observed between other variables. For example, a positive correlation was observed between all life stages of *Stegastes planifrons* and both area of seagrass/SAV (Figure 4.6) as well as length of hard bottom edge. High correlations were measured at the 800 m analysis scale. This highly resident species settles directly onto reefs (Tolimieri 1995, Gutierrez 1998) and spends its benthic life associated with the same coral head or $< \sim 1 \text{ m}^2$ territory (Luckhurst and Luckhurst 1978, Robertson et al. 1981). That either of these landscape variables or this analysis distance have a direct influence on fish abundance is doubtful. These landscape variables may instead be surrogates for, or correlated with, some other environmental factor. Also possibly, some indirect effect may be responsible for the observed correlations.

Did thematic and spatial resolution of maps affect the perceived relationships between fish and their landscapes? In many comparisons, use of different input maps resulted in a changed perception of either the strength of peak correlation at a given scale, or the scale at which peak correlations occurred. The latter case represents a more serious problem in that both the spatial dimensions as well as the intensity of the relationship are perceived differently. Such events call for the most careful consideration of the consequences of relying on a particular map type. These two types of changed perception occurred with different frequency depending on the landscape feature tested. The results indicate that studies relying on the amount of hard bottom edge length and area of sand around reefs need to be especially cautious in interpretation due to the large number of cases where map type changed the perception of the fish and habitat correlation. Correlation between sand/sediment area

and fish assemblages were very sensitive to the spatial resolution of maps used as input data. Spatial resolution of maps often completely changed the perceived relationships between fish and their area of surrounding sand/sediment. In all cases, use of high spatial resolution maps resulted in lower r values or negative r values compared to low spatial resolution maps at the same analysis scale. The level of thematic resolution had no measurable effect on the reported correlation pattern. I believe this may be an artifact of the classification scheme and properties of the local landscapes. There were only two categories at the most detailed level of the scheme, sand and mud, and only very small amounts of mud in the Buck Island study area (Kendall and Miller 2008). This resulted in very similar landscape values whether high or low thematic resolution was used. The perception of the strength of the ecological relationship between fish and hard bottom edge also depended on the type of input maps used. While the general patterns of increasing correlation with scale were generally similar among all four map types, the values of the correlation were often significantly different. Maps of the study site exhibited a doubling of edge length for hard bottom features when high spatial resolution was used to create them (Kendall and Miller 2008). Many reef edges that fish interact with, such as small patch reefs in sand and sand channels in hard bottom, only appeared when high spatial resolution was used. In contrast to these bottom types, the results were quite consistent regardless of the spatial and thematic resolution of the maps used to calculate seagrass/SAV area. Continuous seagrass beds have been shown to be characterized quite consistently at the two map scales used in this study, but patchy beds show large differences (Kendall and Miller 2008). For habitat diversity, all four

map types performed similarly in that none revealed significant correlations with fish variables.

Is there a particular map type that is best to use for landscape ecological studies of reef fish? My results suggest that the answer depends on the landscape variables of interest. For example, I found that maps with high spatial and thematic resolution had most of the significantly highest correlations for comparisons involving hard bottom edge length whereas maps with low spatial and thematic resolution often had the lowest correlations for comparisons involving this landscape variable (Table 4.3). This indicates that studies using hard bottom edge are more likely to yield differing results when using map types of lower spatial or thematic resolution. In contrast, all four map types performed similarly for seagrass/SAV indicating that even simple, inexpensive to produce maps do just as well as highly detailed, expensive and time consuming maps in studies involving this variable. Also of relevance, are the plots of maximum r values by level of organization of fish variables. All map types yielded a similar range of results except for maps with high spatial but low thematic resolution. This map type had lower sensitivity to detecting the highest and lowest peak correlations that were observed more consistently among the other map types. This indicates that mapping only a few bottom types with great spatial detail may be least effective in landscape ecological studies. Why such maps would perform more poorly than those with both low thematic *and* spatial resolution is unclear.

Maximum correlations between landscape variables and individual species achieved a wider range and more extreme values (highest and lowest) than

comparisons involving either guilds or the entire fish assemblage (Figures 4.9a-d). These variables, representing more than a single species, had more moderate peak correlations. This is likely because the habitat preferences and scales of movement of the many species included in such variables get averaged together and limit extreme values. In contrast, individual species had both highest and lowest values since each species interacts with a more discrete set of habitats at similar scales. This pattern did not however, separate the results of individual life stages from all individuals of the focal species, as was expected, nor did it distinguish between mobility guilds and whole community metrics.

Scales of peak correlation were the same for juveniles and adults in over half of the comparisons. The expected result, juveniles having a shorter distance of maximum correlation than adults, rarely occurred (but see Grober-Dunsmore et al. 2007). This suggests that landscape influences on the distribution and abundance of juvenile fish may operate at scales as broad as those for their conspecific adults. Typical scales of landscape interaction for mobility guilds were somewhat more in line with expectations in that transients had broader scales of peak correlation than either resident or mobile fish in a large number of comparisons. Still however, scale of influence was the same for all three mobility guilds in many comparisons again indicating that even resident fish are influenced by their surrounding landscape at distances as broad as those for transients. Despite peak correlation at similar scales, the mechanisms of influences are almost certainly indirect given what is presently known about the very small home range of resident species and juveniles of the six focal species (Itzkowitz 1977, Luckhurst and Luckhurst 1978, Overholtzer and Motta

1999, Bell and Kramer 2000, Watson et al. 2002). Map type generally did not influence the results of peak scale for adult versus juvenile fish. In contrast, results of mobility guild analysis differed in unpredictable ways depending on map type, again indicating that caution be used when studying mobility guilds using a single map type.

I found only a limited subset of the possible functional forms between correlation strength and window size in our study. The flat response is seen in situations for which there is no change in correlation among scales (Figure 4.1b). This can mean no significant correlation at any scale, as was observed for all comparisons involving habitat diversity. It could also indicate a significant correlation of approximately equal strength among all analysis distances, a condition not found in this study but observed between mobile fish abundance and seagrass elsewhere (Grober-Dunsmore et al. 2007). This pattern could also arise if an asymptotic pattern was present and short enough scales were not tested. Conversely, such a pattern could result if the spatial scale was not sufficiently large, so that the analyses had yet to reach a scale at which landscape affected fish distribution. A steadily rising correlation with increasing analysis scale (Figure 4.1c) was observed here between many reef fish and area of seagrass/SAV. A similar pattern was apparent for resident fish abundance and seagrass area in St. John (Grober-Dunsmore et al. 2007), and has also been found in terrestrial studies (Holland et al. 2004, e.g. *Strangalia luteicornis*, *Stictoleptura canadensis*). Such a pattern suggests that the maximum scale of correlation has not yet been reached. A steadily rising correlation could be expected for a species or species group that utilizes a large home range or those indirectly

impacted by processes operating at broad spatial dimensions. Asymptotic curves in strength of correlation with increasing analysis scale (Figure 4.1d) were observed for many comparisons for which correlations were low at short analysis distances then rapidly rose and leveled off at broader analysis distances. This pattern has been observed in St. John between total fish abundance and area of seagrass (Grober-Dunsmore et al. 2007) and in a number of terrestrial systems and taxa (Ricketts et al. 2001 moth species richness and forest cover; Holland et al. 2004, beetles *Stragalepta abbreviata*, *Evodinus monticola* and forest cover). In the present study, this functional form was especially evident in comparisons involving hard bottom edge and maps with the highest spatial and thematic resolution. Maps with less spatial and thematic detail in the same comparison rose to the same scale of maximum correlation more slowly and steadily which indicates that extra caution is required for studies involving this variable. Such species or species groups are likely to be moderate to large home range users. Declining correlations as analysis scale increases are also possible. Such declines could be exponential (Figure 4.1f) or gradual (Figure 4.1e). This was observed more rarely in the present study and generally only occurred in comparisons involving sand/sediment and maps with low spatial resolution (e.g. Figure 4.9). This pattern has also been seen in several terrestrial systems and taxa (Pearman 2002, omnivorous birds with primary forest cover; Steffen-Dewenter 2003, species richness of bees and wasps and habitat diversity; Holland et al. 2004, beetle abundance *Microgoes oculatus* and area of forest cover). These species typically have a small home range and are not even indirectly influenced by the resource across broader distances. Also possible are more discrete peaks in correlation strength at

intermediate scales (Figure 4.1a). This type of response would be expected for species or species groups with well defined home range of intermediate size and has been observed in marine (Grober-Dunsmore et al. 2007, species richness of fish and seagrass area) and terrestrial systems (Pearman 2002, bird guilds and primary forest; Holland et al. 2004, beetle abundance *Urographis fasciatus*, *Gaurotes cyanipennis*, *Urgleptes signatus* and forest cover). Such well defined and more discrete peaks were not found in the present study. This may indicate that the reef fish community and species variables tested are more flexible in home range size and responses to surrounding habitat, or are influenced by a variety of direct and indirect processes operating at a number of spatial scales relative to organisms with more discrete landscape requirements.

A key message of the present research is that detection of these response curves and their shape depends on several factors including the type of map that is used to generate the landscape variables, the range of scales tested, and the interval or distance between analysis scales. Here, all three of these situations arose. Map type resulted in either asymptotic or steadily rising correlations between the same variables (e.g. Figure 4.8). Correlations steadily rising at the broadest scales evaluated in the present study may level off (asymptotic) or decline (peak) once even longer analysis scales are considered. Shortening the interval between analysis distances may also allow better identification of peaks for species or species groups with very discrete home range sizes.

This study used $|r| > 0.2$ as the cutoff for values of ecological significance because of the very low SEM values that resulted from the resampling procedure.

This limited results and discussion to a much more conservative, although admittedly arbitrary, standard than the conventionally used $p < 0.05$. If an even more conservative value of $|r| > 0.3$ ($r^2 = 0.09$, or 9% of the relationship between the variables explained) were used, all of the general patterns observed in the study would remain the same although fewer of the comparisons would be considered ecologically significant. Similarly, if a lower value such as $|r| > 0.1$ were used, all of the general findings would remain consistent, only more of the very low correlations would be discussed despite their extremely low explanatory power and ecological relevance. My adoption of the more conservative $|r| = 0.2$ standard does limit the probability of type I errors influencing our results.

Most prior landscape ecological studies, whether on terrestrial or marine ecosystems base results on one type of map. Little consideration appears to have been given to the influence of map type on the conclusions reached. However, terrestrial investigations have shown that the characteristics of input maps can influence results of landscape ecology studies. For example, Stohlgren et al. (1997) found that the use of maps with low spatial resolution dramatically underestimated (35% lower) overall plant community diversity, the number of habitat patches, and total plant species richness relative to high resolution maps. Karl et al. (2000) found that models predicting bird distribution using maps with fewer thematic categories generally performed better than those using many themes. Results here also suggest that use of a single map type in the marine environment can also lead to an incomplete or even incorrect perception (i.e. undetected, weakly measured, inversely signed, thought to occur at the wrong scale) of habitat utilization and scale at which

organisms interact with their landscape. This is less of a problem if landscape features of interest are characterized similarly across scales but can be a big concern of landscape features are sensitive to thematic and spatial scale of representation.

Based on the findings here, the following advice can be given to those interested in mapping coral reef ecosystems to study landscape ecology of reef fish or making spatially explicit management decisions using benthic maps as an information input. Hard bottom should be mapped with high spatial resolution above all else since this most affects reef edge depictions. Time and money permitting, hard bottom should be mapped with high thematic resolution as well and separated into its various reef types. Many studies are presently concerned with hard bottom edge and proximity to hard bottom habitat (Sweatman and Robertson 1994, Dorenbosch et al. 2005, Wernberg et al. 2006, Vanderklift et al. 2007, Valentine et al. 2007).

Extrapolating their mostly *in situ* studies to landscape scales using benthic maps carries with it particular concerns. Sand should be mapped with high spatial resolution to pick up key features such as sand channels in hard bottom and halo's separating hard bottom from seagrass (Kendall and Miller 2008). Quite different conclusions are likely to be drawn regarding fish-landscape correlations when less spatially resolved maps are used. In contrast to these bottom types, seagrass mapped at coarse thematic and spatial resolution appear to effectively evaluate the landscape ecology of a variety of fish species and will result in similar values when more detailed maps are used. Given these findings, prior seagrass studies probably do not need to be concerned about their results changing if different map types were used (e.g. Pittman et al. 2004, Kendall 2005, Grober-Dunsmore et al. 2007). Results

involving hard bottom or sand however could change measurably were different landscape maps used as input. Habitat diversity is simply not representative of fish diversity, or any other measure of the fish community, at any scale and should not be considered as a surrogate or proxy variable. To keep these recommendations in perspective however, landscape variables that were used here were for common bottom features. Habitat specialists that are obligate users of a particular reef type for example would need to be studied with a map of sufficient spatial and thematic complexity to capture that feature.

Table 4.1: Scale of maximum correlation between fish and landscape variables. Values are in meters. Comparisons that yielded different results for one or more maps types are denoted with an asterisk (*). Comparisons that had no correlations above $r = 0.2$ are denoted with a less than symbol (<). All figures are provided in the Appendix. Figure numbers (1-4) and letters (a-z) are given and denote corresponding landscape and fish variables respectively.

Fish variables		Habitat Diversity	Seagrass/ SAV Area	Sand/Sedi- ment Area	Hard Bottom Edge Length	
		Appendix Figures 1	Appendix Figures 2	Appendix Figures 3	Appendix Figures 4	Fig.
Whole Community	Fish abundance	<	<	<	<	a
	Species richness	<	800	800*	800*	b
Mobility Guild	Resident fish abundance	<	<	25*	<	c
	Resident species richness	<	800	<	800	d
	Mobile fish abundance	<	<	<	<	e
	Mobile species richness	<	<	<	50*	f
	Transient fish abundance	<	<	800*	<	g
	Transient species richness	<	<	800*	<	h
Species	<i>Acanthurus coeruleus</i> juvenile abund.	<	<	<	800*	i
	<i>Acanthurus coeruleus</i> adult abund.	<	<	<	800*	j
	<i>Acanthurus coeruleus</i> total abund.	<	<	<	800*	k
	<i>Cephalopholus fulvus</i> juvenile abund.	<	800	25*	800*	l
	<i>Cephalopholus fulvus</i> adult abund.	<	800	100*	800*	m
	<i>Cephalopholus fulvus</i> total abund.	<	800	25*	800*	n
	<i>Haemulon flavolineatum</i> juvenile abund.	<	<	<	<	o
	<i>Haemulon flavolineatum</i> adult abund.	<	800	<	50*	p
	<i>Haemulon flavolineatum</i> total abund.	<	800	<	50*	q
	<i>Ocyurus chrysurus</i> juvenile abund.	<	800*	<	<	r
	<i>Ocyurus chrysurus</i> adult abund.	<	<	<	<	s
	<i>Ocyurus chrysurus</i> total abund.	<	100	<	<	t
	<i>Sparisoma viride</i> juvenile abund.	<	800	<	800*	u
	<i>Sparisoma viride</i> adult abund.	<	400	<	800*	v
	<i>Sparisoma viride</i> total abund.	<	<	<	800*	w
	<i>Stegastes planifrons</i> juvenile abund.	<	800	<	800*	x
	<i>Stegastes planifrons</i> adult abund.	<	800	<	800*	y
	<i>Stegastes planifrons</i> total abund.	<	800	<	800*	z

Table 4.2: Tally of the types of differences found in correlations due to use of different input map types. Values are counts of the two types of differences that can occur when use of different input maps did not yield the same result. Results are separated by landscape variables.

	Habitat Diversity	Seagrass/SAV	Sand/Sediment	Hard Bottom Edge Length
Peak is at same scale as maximum $ r $, but significantly lower value ($p < 0.001$)	0	7	0	24
Peak is at a different scale than that of maximum $ r $	0	4	14	17

Tables 4.3a-b: Tally of the number of times each map type had the highest (a) or lowest (b) $|r|$ value when a significant result was present. Results are separated by landscape variables.

a.	Map Resolution	Habitat Diversity	Seagrass/SAV	Sand/Sediment	Hard Bottom Edge Length
Significantly highest $ r $ value	High Spatial High Thematic	0	0	0	5
	High Spatial Low Thematic	0	0	0	0
	Low Spatial High Thematic	0	0	0	1
	Low Spatial Low Thematic	0	1	0	0

b.	Map Resolution	Habitat Diversity	Seagrass/SAV	Sand/Sediment	Hard Bottom Edge Length
Significantly lowest $ r $ value	High Spatial High Thematic	0	0	0	1
	High Spatial Low Thematic	0	0	0	3
	Low Spatial High Thematic	0	0	0	0
	Low Spatial Low Thematic	0	0	0	5

Table 4.4: Relative scale of maximum $|r|$ values for resident, mobile, and transient fish within the four map types.

Hard bottom edge length				
	High spatial	High spatial	Low spatial	Low spatial
	High thematic	Low thematic	High thematic	Low thematic
Fish abundance	$R=M<T$	$M<R=T$	$R=M<T$	$R=M<T$
Species richness	$R=M=T$	$R=M=T$	$R=M<T$	$R=M=T$

Seagrass/SAV				
	High spatial	High spatial	Low spatial	Low spatial
	High thematic	Low thematic	High thematic	Low thematic
Fish abundance	$R=M=T$	$R=M<T$	$M<R<T$	$R<M<T$
Species richness	$R=M=T$	$R=M<T$	$R<M=T$	$R<M=T$

Sand/Sediment				
	High spatial	High spatial	Low spatial	Low spatial
	High thematic	Low thematic	High thematic	Low thematic
Fish abundance	$R=M=T$	$T<R=M$	$R=M=T$	$R=M<T$
Species richness	$M<R=T$	$T<R=M$	$R=M=T$	$R=M=T$

Table 4.5: Relative scale of maximum $|r|$ values for juveniles versus adults of each of the six focal species within the four map types.

Hard bottom edge length				
	High spatial High thematic	High spatial Low thematic	Low spatial High thematic	Low spatial Low thematic
<i>Acanthurus coeruleus</i>	J=A	J=A	J=A	A<J
<i>Cephalopholis fulvus</i>	J=A	J=A	J=A	J=A
<i>Haemulon flavolineatum</i>	J=A	J=A	J=A	J=A
<i>Ocyurus chrysurus</i>	J<A	J<A	A<J	A<J
<i>Sparisoma viride</i>	J=A	A<J	J=A	A<J
<i>Stegastes planifrons</i>	J<A	J=A	J=A	J=A

Seagrass/SAV				
	High spatial High thematic	High spatial Low thematic	Low spatial High thematic	Low spatial Low thematic
<i>Acanthurus coeruleus</i>	A<J	A<J	A<J	A<J
<i>Cephalopholis fulvus</i>	J=A	J=A	J=A	J=A
<i>Haemulon flavolineatum</i>	J=A	J=A	J=A	J=A
<i>Ocyurus chrysurus</i>	A<J	A<J	A<J	A<J
<i>Sparisoma viride</i>	A<J	A<J	A<J	A<J
<i>Stegastes planifrons</i>	J=A	J=A	J=A	J=A

Sand/Sediment				
	High spatial High thematic	High spatial Low thematic	Low spatial High thematic	Low spatial Low thematic
<i>Acanthurus coeruleus</i>	A<J	A<J	J=A	J=A
<i>Cephalopholis fulvus</i>	A<J	A<J	J<A	J<A
<i>Haemulon flavolineatum</i>	J=A	J=A	J<A	J<A
<i>Ocyurus chrysurus</i>	J=A	J=A	J=A	J=A
<i>Sparisoma viride</i>	J=A	J=A	J=A	J=A
<i>Stegastes planifrons</i>	J<A	J<A	J<A	J<A

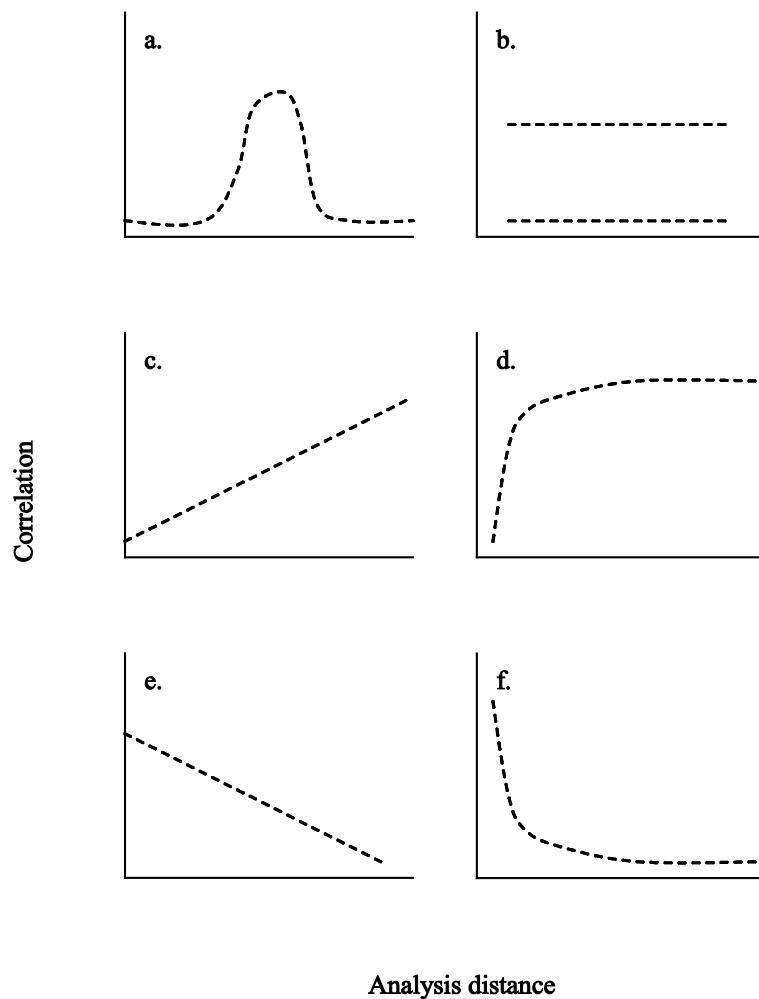


Figure 4.1: Potential relationships between the strength of organism-landscape correlations and the scale (i.e. analysis distance) at which landscape variables are calculated. Only positive correlations are shown for simplicity: a) clear peak in correlation at a discrete scale, b) flat line of uniform correlation at all scales (lower line is the case of no correlation at any scale, upper line is the case of the same correlation at all scales), c) steady increase in correlation with scale, d) asymptotic or rapid increase in correlation with scale then flattening out, e) steady decline with scale, and f) exponential or rapid decline in correlation with distance.

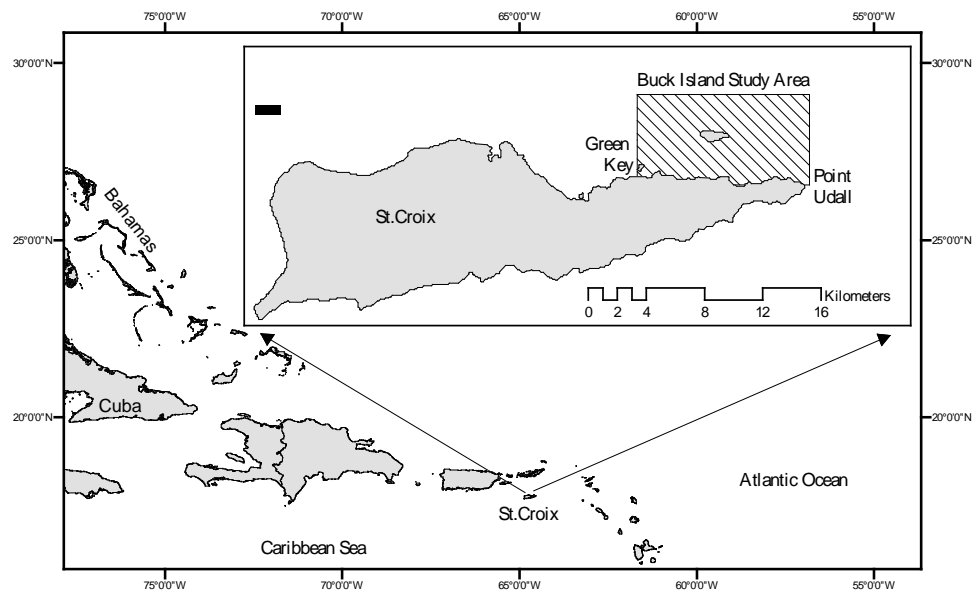


Figure 4.2: Buck Island study area, St.Croix, US Virgin Islands.

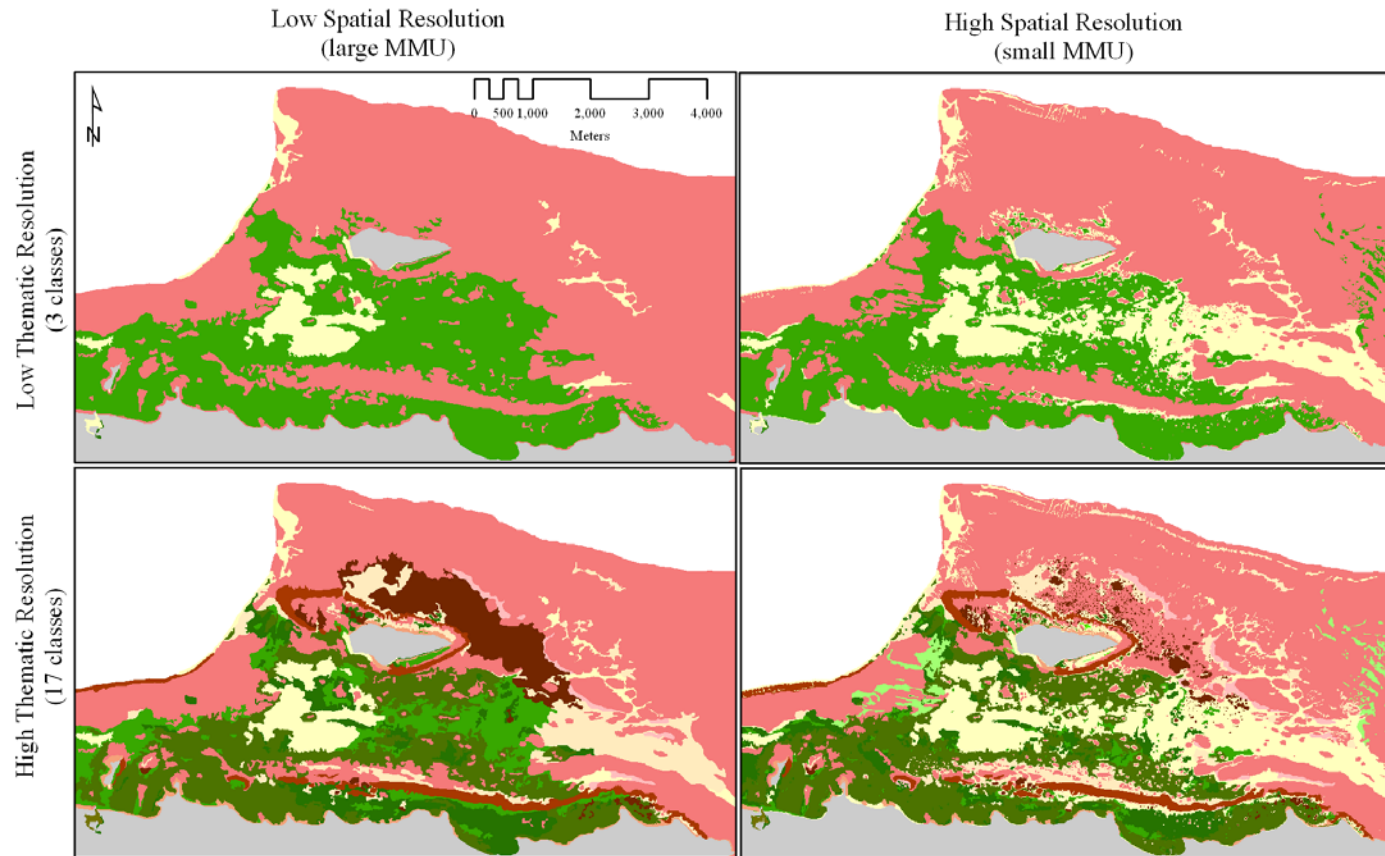


Figure 4.3: Four map types of the study region. Clockwise from upper left is the map with low spatial and thematic resolution, low spatial but high thematic resolution, high spatial and thematic resolution, and high spatial but low thematic resolution. Grey denotes land. White denotes unmapped area beyond the shelf edge. Green tones denote seagrass/SAV categories. Tans denote sand/sediment categories. Reds denote hard bottom categories.

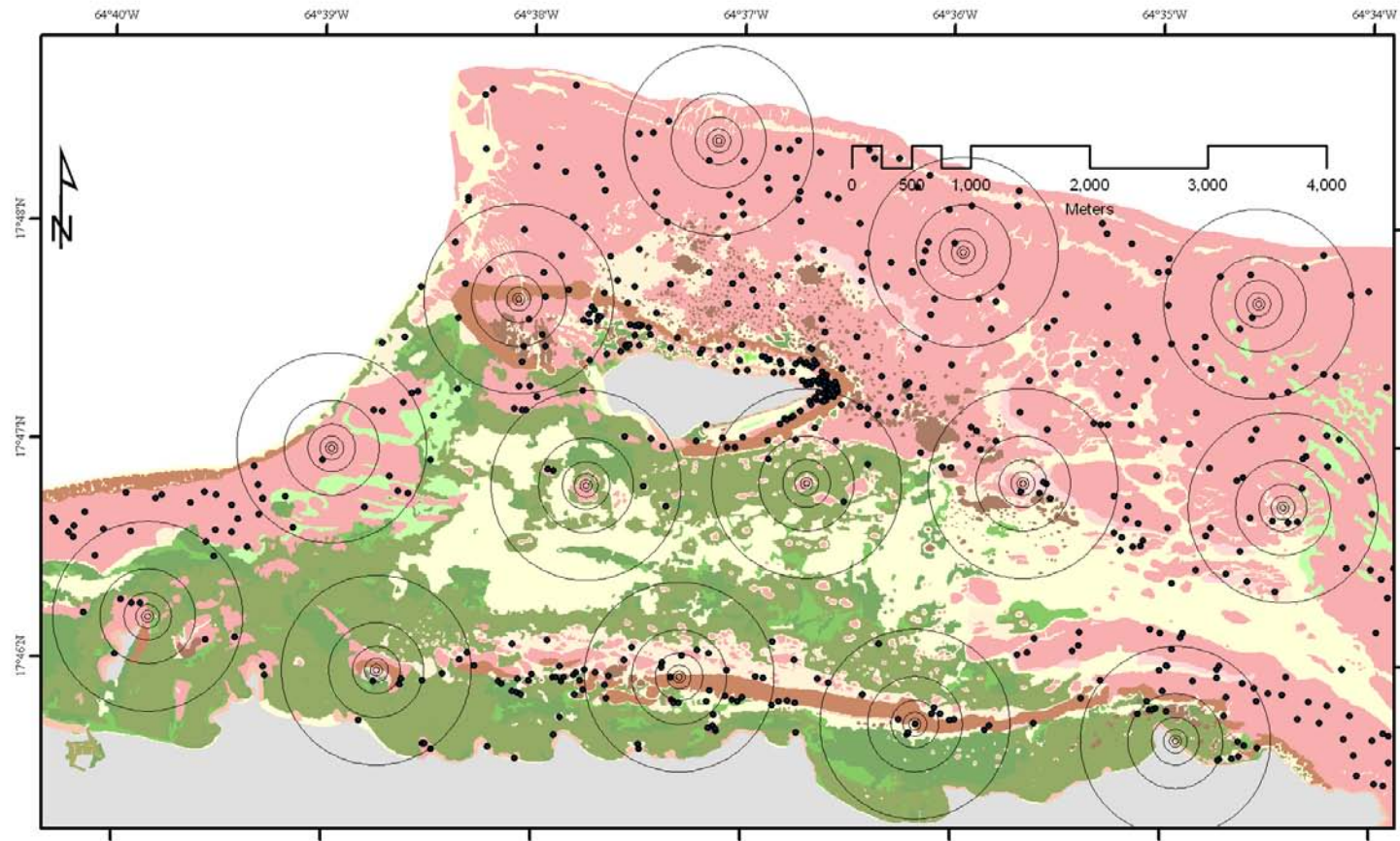


Figure 4.4: Locations of fish survey sites, denoted by black dots, in the Buck Island study area. A set of 14 randomly selected, non-overlapping sites with their corresponding analysis radii (25, 50, 100, 200, 400, 800 m) are shown. Backdrop is the benthic map with high spatial and thematic resolution.

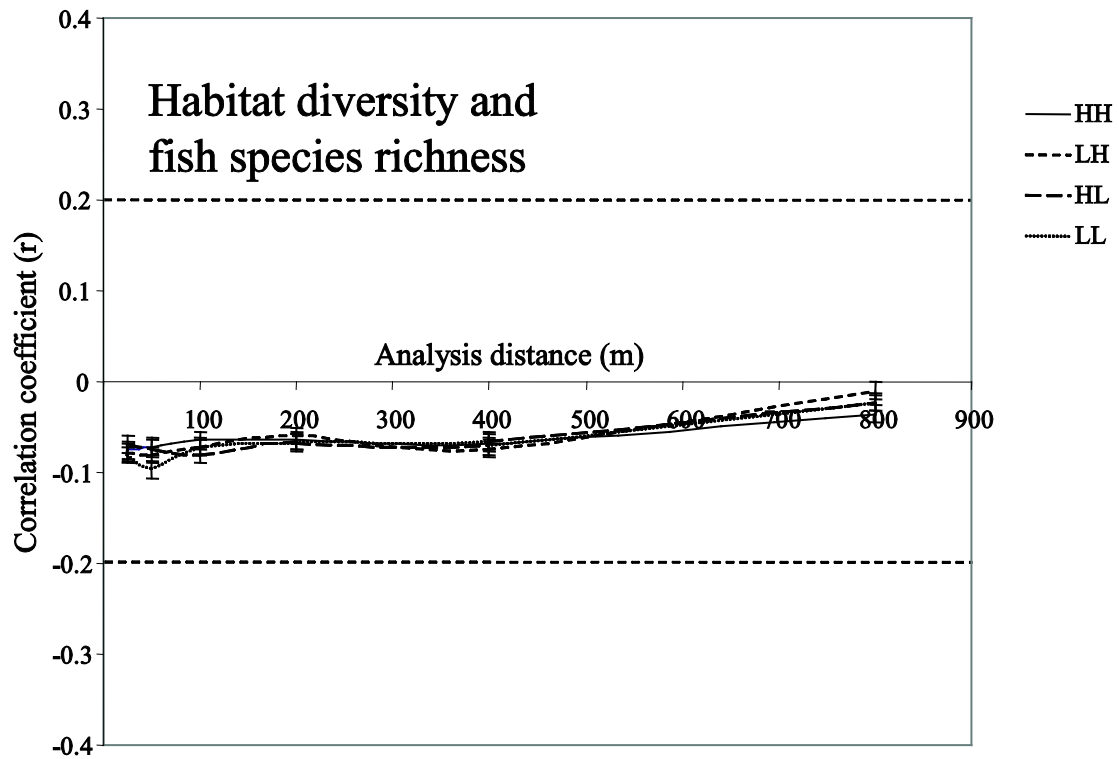


Figure 4.5: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution.

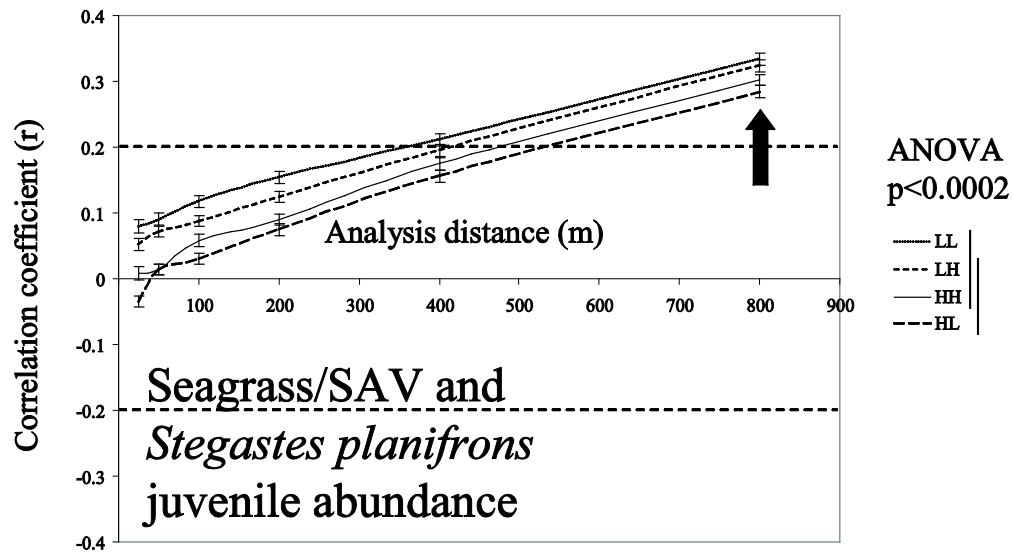


Figure 4.6: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution. Where a significant correlation was found ($|r| > 0.2$), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation.

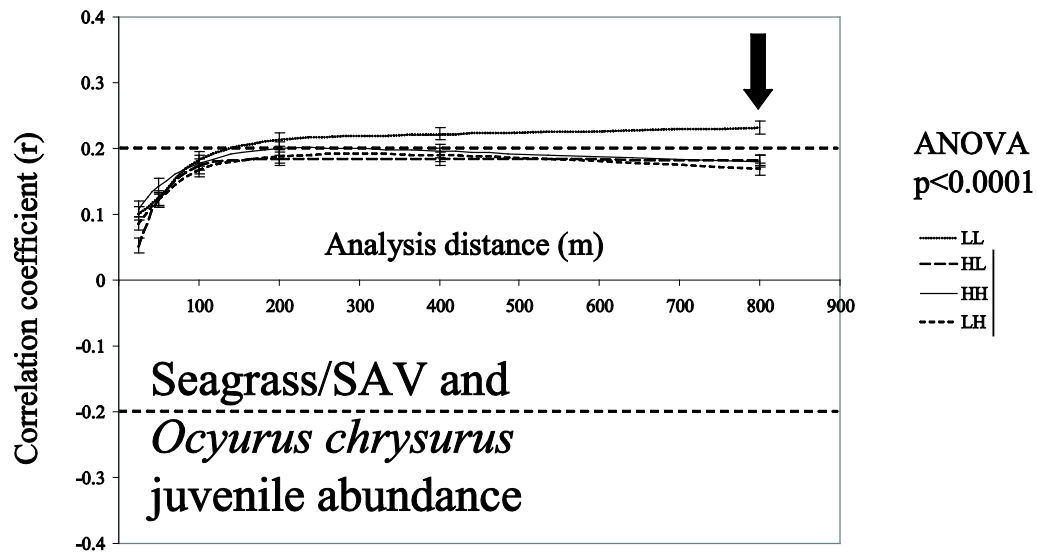


Figure 4.7: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution. Where a significant correlation was found ($|r| > 0.2$), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation.

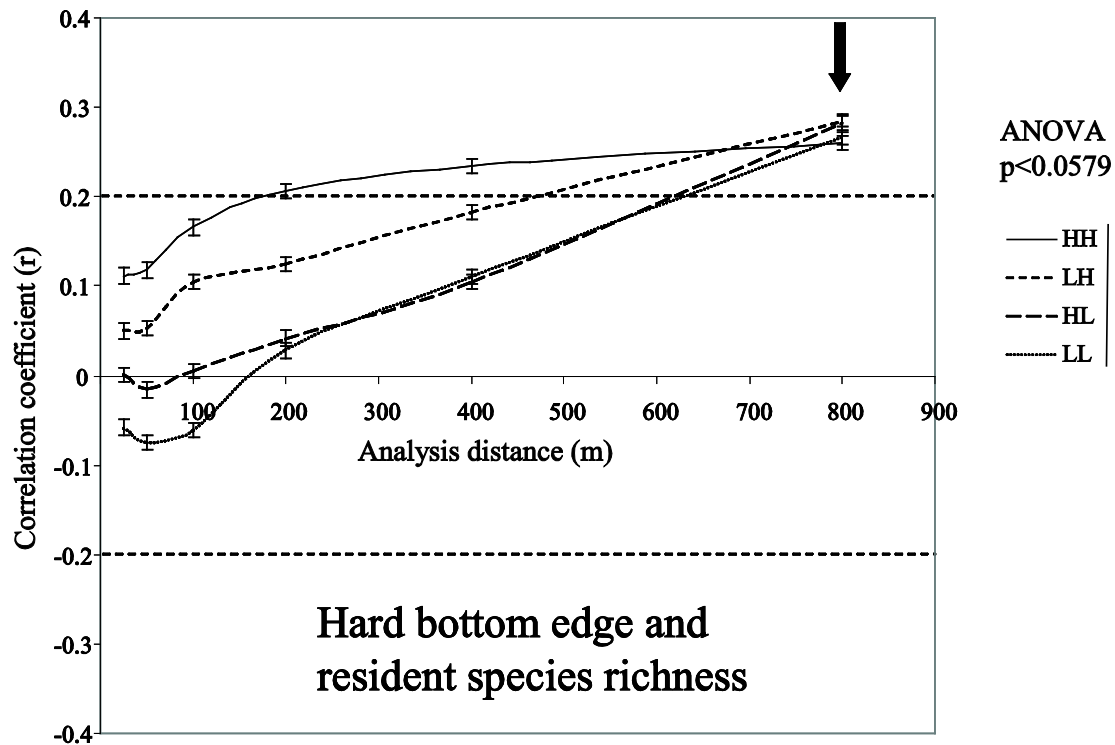


Figure 4.8: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution. Where a significant correlation was found ($|r| > 0.2$), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation.

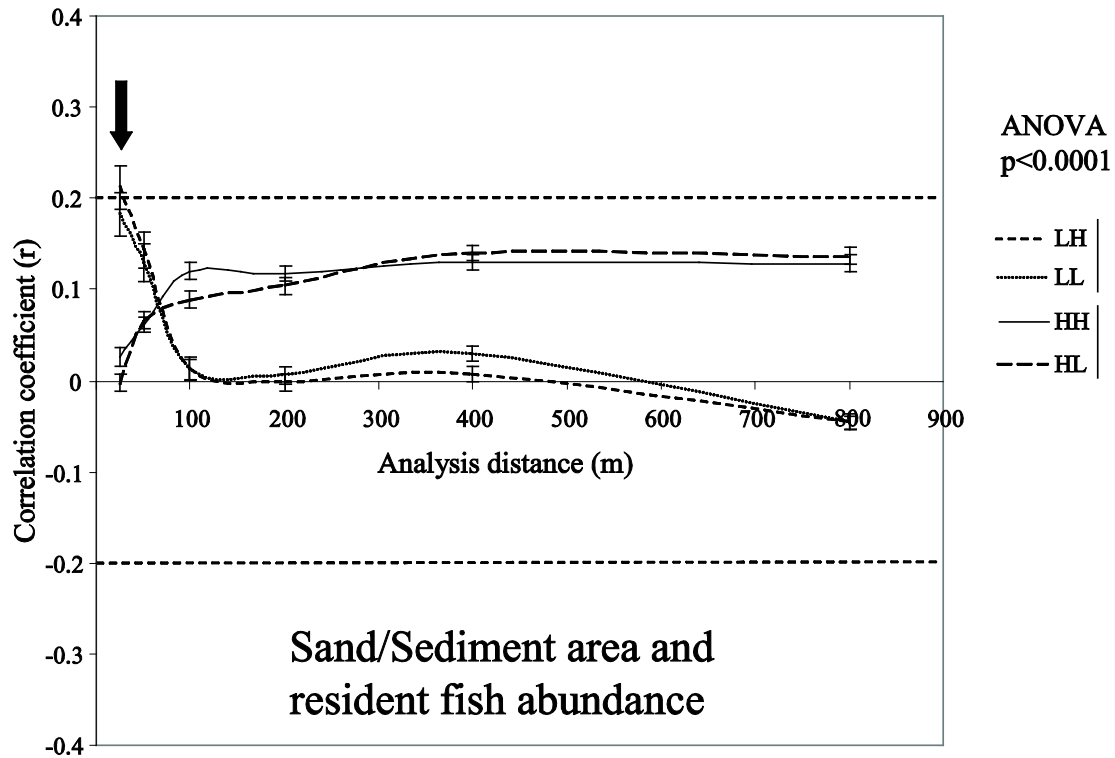


Figure 4.9: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution. Where a significant correlation was found ($|r| > 0.2$), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation.

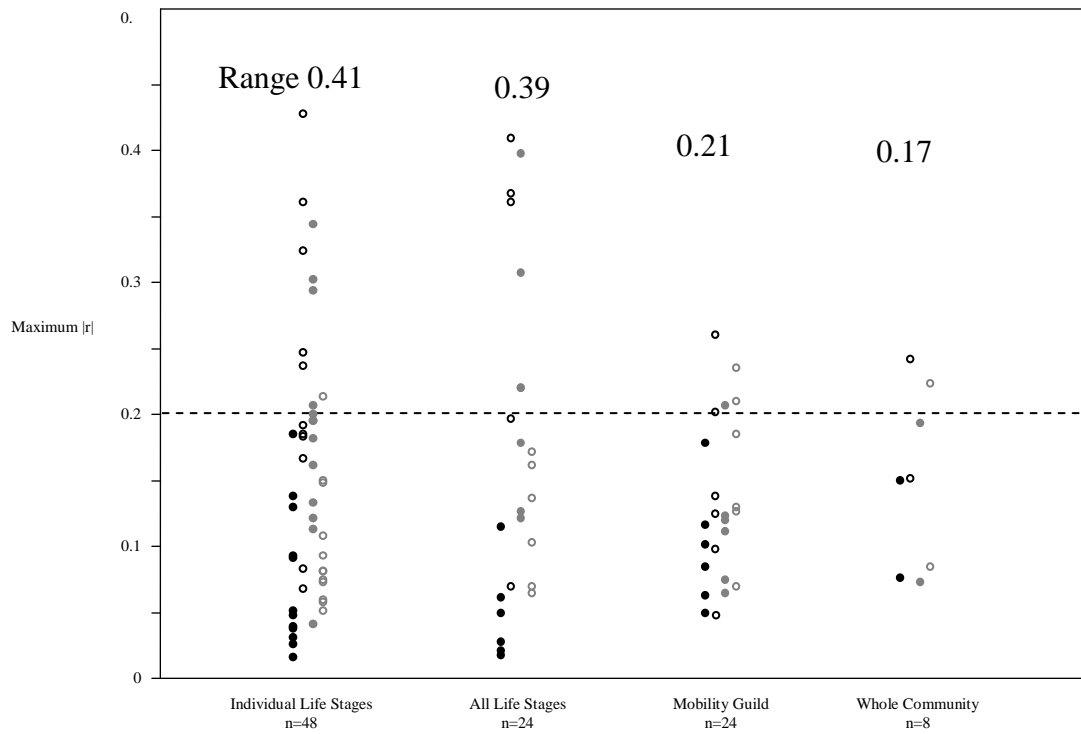


Figure 4.10a: Maximum $|r|$ values for all 104 x and y variables investigated in the study using maps with high spatial and thematic resolution. Results are grouped by level of organization of the fish variables. Symbols denote the landscape variables associated with each $|r|$ value. Black dots denote habitat diversity, black circles denote hard bottom edge length, grey dots denote seagrass/SAV, and grey circles denote sand/sediment.

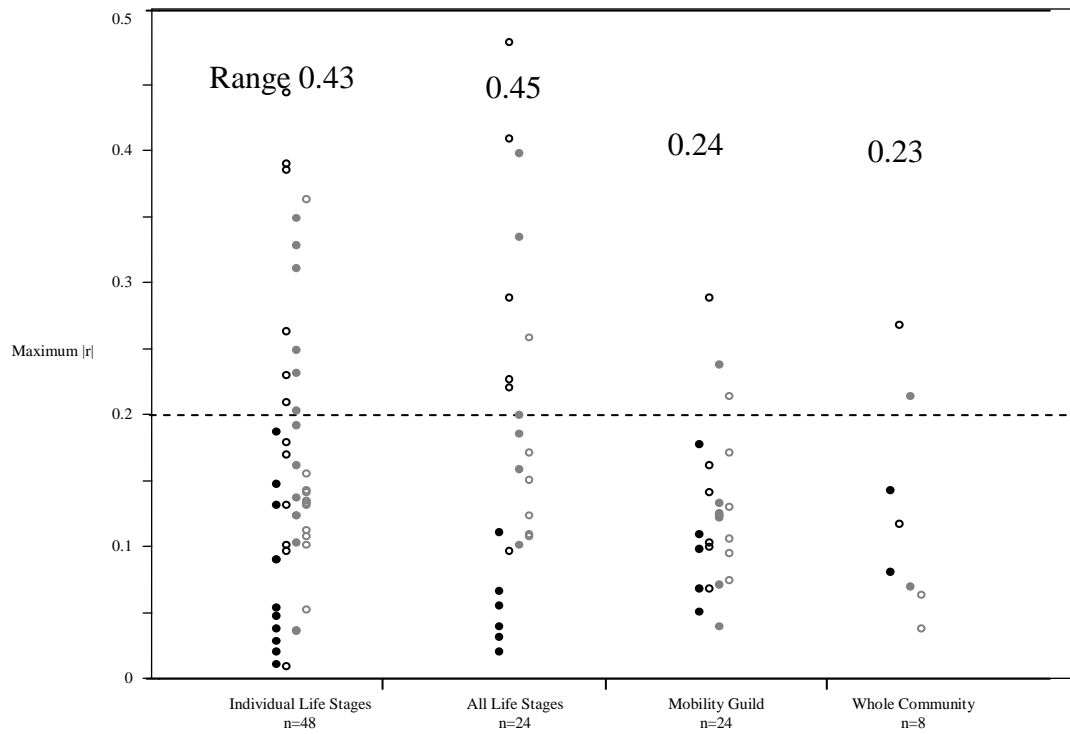


Figure 4.10b: Maximum $|r|$ values for all 104 x and y variables investigated in the study using maps with low spatial and high thematic resolution. Results are grouped by level of organization of the fish variables. Symbols denote the landscape variables associated with each $|r|$ value. Black dots denote habitat diversity, black circles denote hard bottom edge length, grey dots denote seagrass/SAV, and grey circles denote sand/sediment.

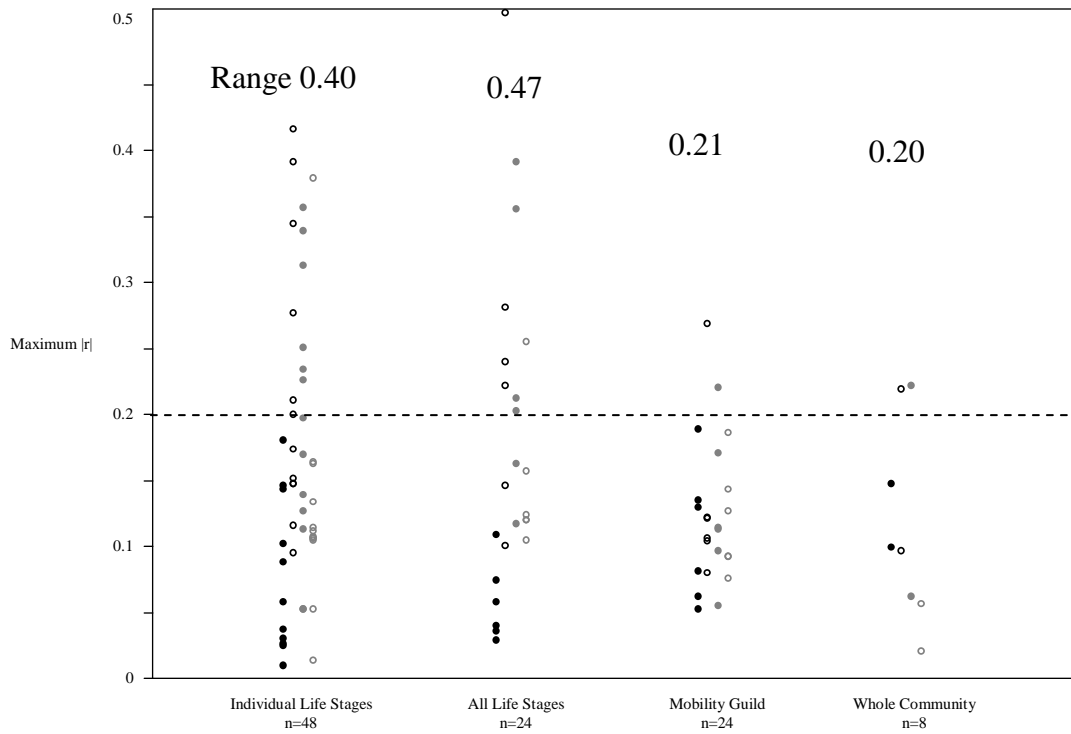


Figure 4.10c: Maximum $|r|$ values for all 104 x and y variables investigated in the study using maps with low spatial and thematic resolution. Results are grouped by level of organization of the fish variables. Symbols denote the landscape variables associated with each $|r|$ value. Black dots denote habitat diversity, black circles denote hard bottom edge length, grey dots denote seagrass/SAV, and grey circles denote sand/sediment.

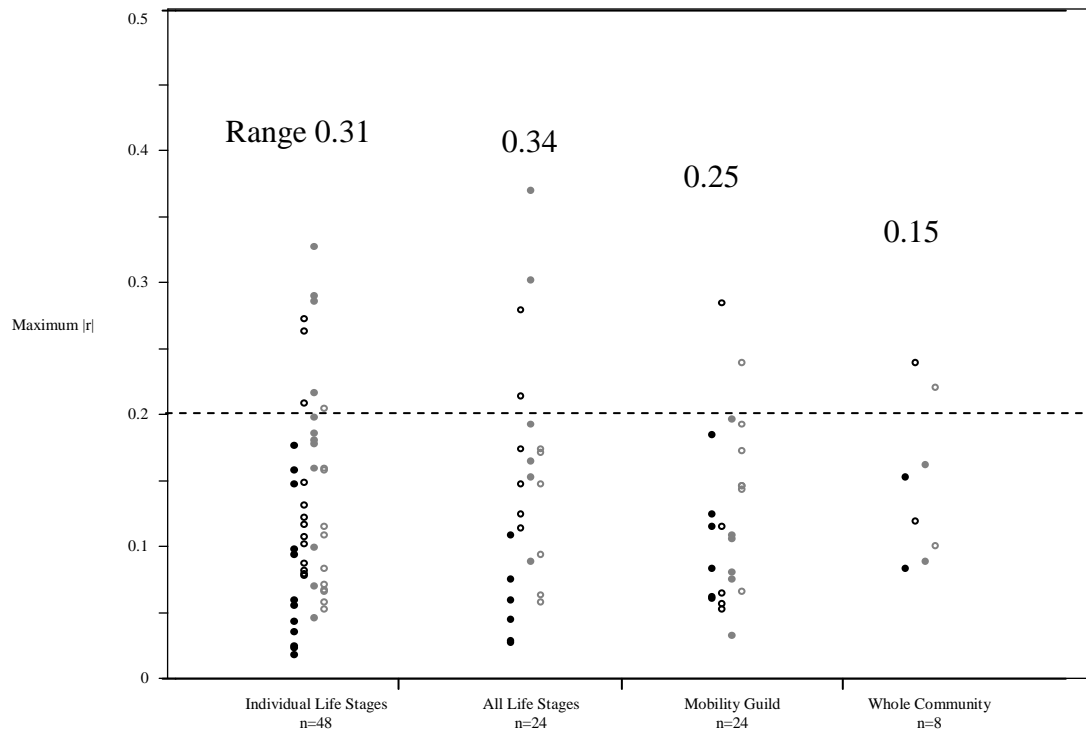


Figure 4.10d: Maximum $|r|$ values for all 104 x and y variables investigated in the study using maps with high spatial and low thematic resolution. Results are grouped by level of organization of the fish variables. Symbols denote the landscape variables associated with each $|r|$ value. Black dots denote habitat diversity, black circles denote hard bottom edge length, grey dots denote seagrass/SAV, and grey circles denote sand/sediment.

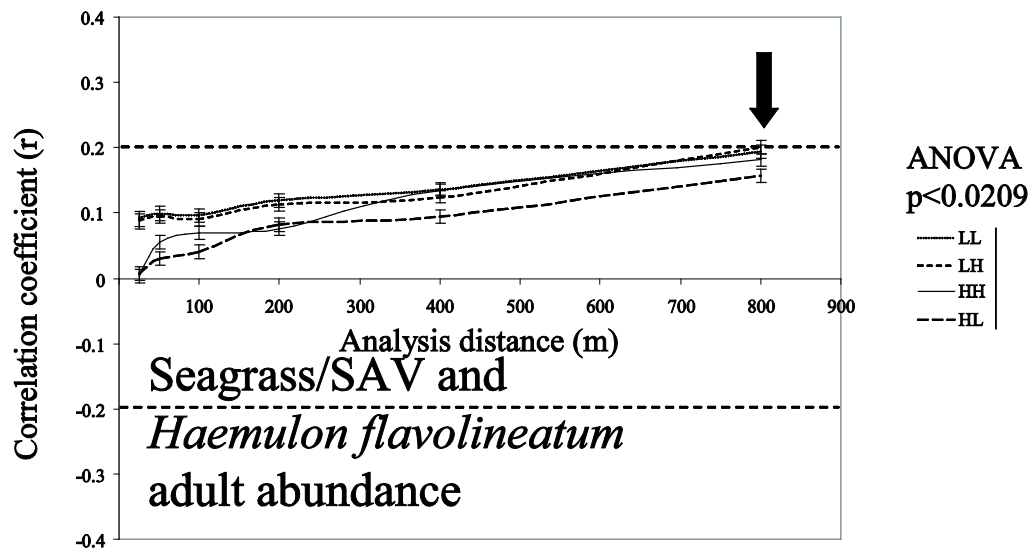


Figure 4.11: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution. Where a significant correlation was found ($|r| > 0.2$), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation.

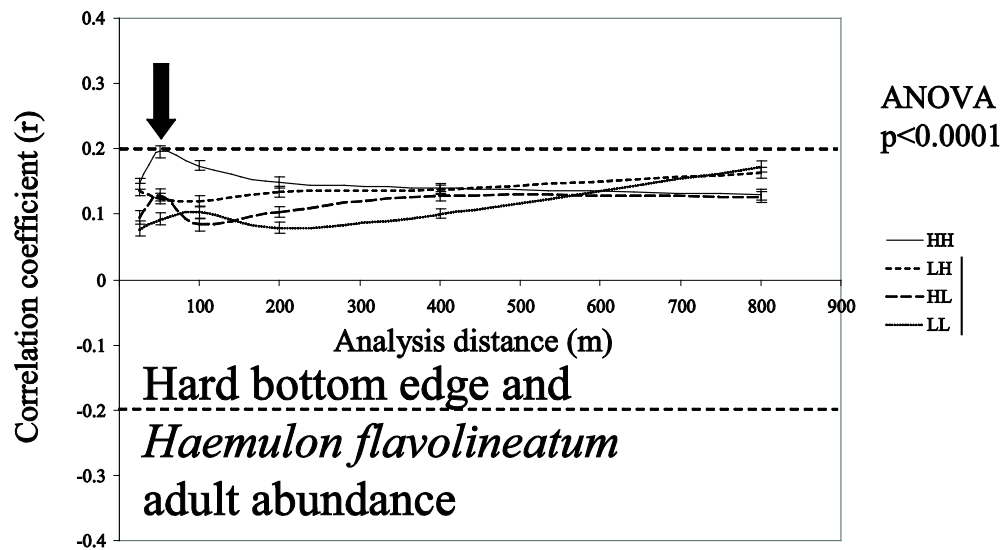


Figure 4.12: Correlation plot of analysis distance by r for all four maps types. HH denotes the map with high spatial and thematic resolution. LH denotes the map with low spatial and high thematic resolution. HL denotes the map with high spatial and low thematic resolution. LL denotes the map type with low spatial and thematic resolution. Where a significant correlation was found ($|r| > 0.2$), the scale with the strongest relationship is noted with the black arrow. Vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation.

Chapter 5: Summary and Conclusions

Benthic maps are essential tools for marine scientists and managers. Map characteristics are controlled by the spatial and thematic resolutions selected during map production. The implications of these production decisions on the inferences that can be drawn from the maps are poorly quantified and understood. This dissertation addressed this need by evaluating the differences among common map types, considering how map type affects inferences of fish and benthic communities at the patch level, and then evaluating the influence of map type on ecological neighborhoods of many species and communities of reef fish.

In Chapter 2, four maps of a coral reef ecosystem at St. Croix, U.S. Virgin Islands were created using two levels of both spatial and thematic resolution. Differences among the maps were quantified using indices from the field of landscape ecology. The results indicated that inferences regarding the structure and physical organization of reef ecosystems were sensitive to changes in spatial and thematic resolution of the maps characterizing them. Significant differences were found for 28 out of 44 comparisons among independent bottom types and metrics describing landscape structure. Increasing thematic resolution greatly increased the number of map polygons, total edge length of polygons, and the diversity of maps by splitting the landscape into more categories. Changing the spatial resolution resulted in disproportionate changes in bottom types for nearly all metrics considered. When spatial resolution was increased by mapping smaller features, dominant bottom types such as hard bottom became less dominant and rare bottom types became more

common. For metrics based on whole maps, the range of values observed in total number of polygons, average feature size, and total edge spanned an order of magnitude among maps. Hard bottom in general, especially the patch reefs and colonized pavement components, as well as sand areas and patchy features were among the most sensitive to change in spatial resolution. In contrast, linear reef and continuous seagrass features were characterized quite consistently regardless of spatial resolution used in mapping. The findings demonstrate that the spatial and thematic resolution of benthic maps imposed during their creation can dramatically influence some, but not all map characteristics. This led to the expectation that results of ecological studies reliant on those characteristics would vary considerably depending on the thematic and spatial characteristics of the map used as input.

In Chapter 3, the possibility that map type could influence outcomes of ecological studies was investigated at the patch level for reef types. Multivariate analyses were used to understand the relationships among fish assemblages, local habitat variables, and the reef types they are found in as depicted in the benthic maps from Chapter 2. In those maps, benthic features were attributed with one of 6 reef types in addition to lagoon versus shelf zonation. Ordination based on fish assemblages and the environmental data did not result in well separated groups of sites which indicated that a continuum of local fish and environmental conditions exists across the study area. In general, mapped reef types were not associated with distinct values of either local environmental variables or fish assemblages. Reef types differed along continuums and had much overlap in ordination plots based on both fish assemblage and benthic characteristics. Reef types grouped more loosely by their

fish assemblages than by local environmental characteristics. Ordination patterns involving reef type were largely the same for maps with both low and high resolution. This was somewhat surprising given the large differences detected among 3 of the six reef types measured in Chapter 2. In contrast, shelf position, which was independent of map scale in this study, showed clear patterns with both environmental variables and fish assemblage composition respectively. In general, the results suggest that knowledge of the overall fish assemblage or fine-scale environmental characteristics could not be used to predict reef type or vice versa. Furthermore, spatial scale of benthic maps did not affect the fish community results when analyses were conducted at the patch level.

Chapter 4 represented a more advanced, multi-scale landscape analysis and retained the central theme in the dissertation of examining the influence of map type on ecological investigations. Correlations between fish assemblages and surrounding landscape variables were measured using univariate linear regression for a range of scales between 25 and 800 m. The strength of the associations as a function of scale achieved one of 6 response curve forms and were used to identify the scale that best correlates fish with their surrounding habitat. Dependent variables in the analysis were overall species richness, total fish abundance, and species richness and abundance of fish in the mobility guilds: transient, mobile, and resident. Also considered was the abundance of six common reef fish species respectively that were further separated into total, juvenile, and adult categories. Independent or landscape variables considered were area of seagrass or submerged aquatic vegetation (SAV), length of hard bottom edge, area of sand or unconsolidated sediment, and habitat

diversity. To evaluate the influence of map type, the landscape variables were calculated based on the four separate benthic maps from Chapter 2. Individual landscape variables explained a maximum of only 25 % of the variability in fish distributions. Habitat diversity was a poor predictor of all aspects of the fish community. Seagrass/SAV and Sand/sediment area predicted distribution of many fish, not just those considered obligate users. Length of hard bottom edge was correlated with more of the fish variables than any other landscape feature tested. Landscape correlations for individual species achieved a wider range and more extreme values than comparisons involving mobility guilds or the entire fish assemblage. Scales of peak correlation were the same for juveniles and adults in over half of the comparisons. Transients had broader scales of peak correlation than either resident or mobile fish in a large number of comparisons. Use of different input maps resulted in a changed perception of either the strength of peak correlation at a given scale, or the scale at which peak correlations occurred for many comparisons involving hard bottom edge length and area of sand. This was to be expected given that Chapter 2 revealed significant differences in perimeter length of several hard bottom categories and nearly significant differences in area of sand based on MMU. In contrast, results of fish neighborhood analyses were quite consistent in strength and scale regardless of map type for comparisons involving seagrass/SAV area. This was somewhat surprising given that submerged vegetation, especially patchy seagrass was characterized quite differently in Chapter 2 depending on MMU.

The dissertation represents an unprecedented investigation of the influence of map resolution on landscape ecological analyses of a reef ecosystem. Understanding

the influence of map type is essential to interpret the results of such studies and to correctly apply the findings to management strategies. Next steps include publication of the individual core chapters (2-4) in peer reviewed journals and extending the research topics investigated here. Chapter 2, on the effects of thematic and spatial resolution on the maps themselves is published in *Marine Geodesy* (Kendall and Miller 2008). Chapter 3, the multivariate investigation on relationships among fish assemblages, local habitat variables, and the reef types they are found in as depicted in the benthic maps, will be submitted to *Coral Reefs*. Chapter 4, on the scale and strength of correlations between fish assemblages and their surrounding landscape variables based on different types of maps will be submitted to *Ecological Monographs*.

Three main lines of research emerge from the dissertation. First, the analyses in the dissertation were based on a dataset of opportunity. The dataset that was used was a random stratified design intended for inventory and monitoring of the reef fish community around BIRNM. The design resulted in hundreds of sample sites within a diversity of reef types that were surrounded by a wide spectrum of landscape features. This diverse group of landscape settings coupled with fish surveys enabled a wide range of landscape questions and variables to be investigated. The results presented here provide a starting place to design more focused sampling strategies to test specific hypotheses with improved experimental control and statistical power.

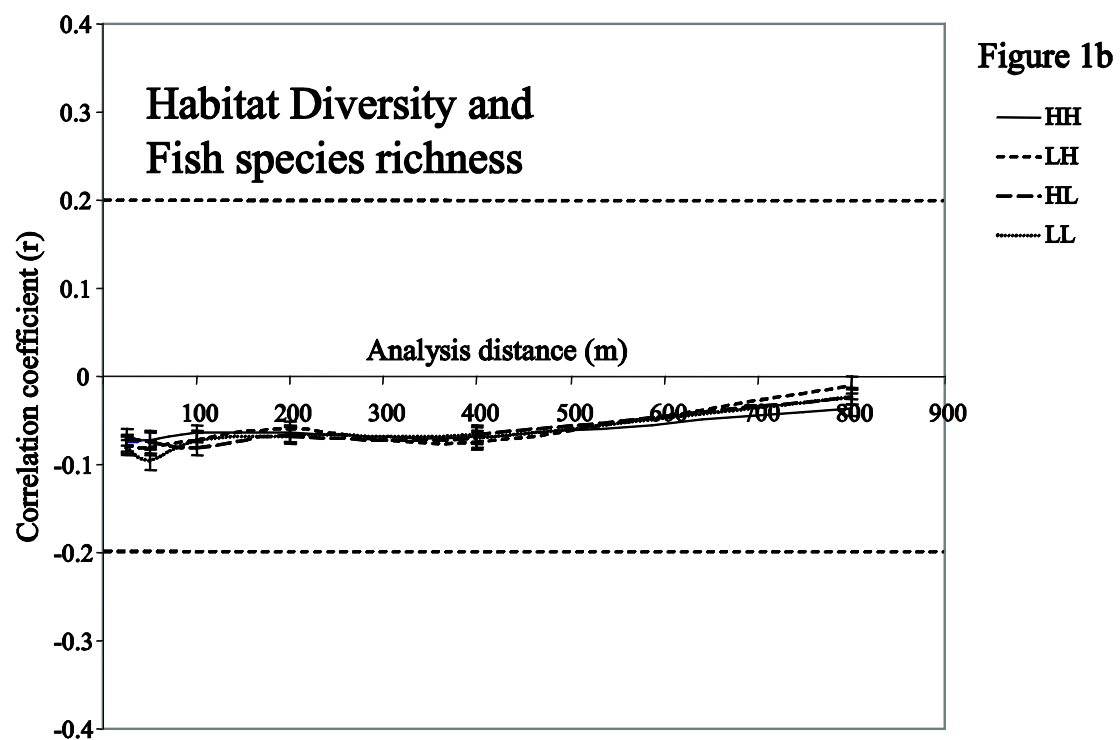
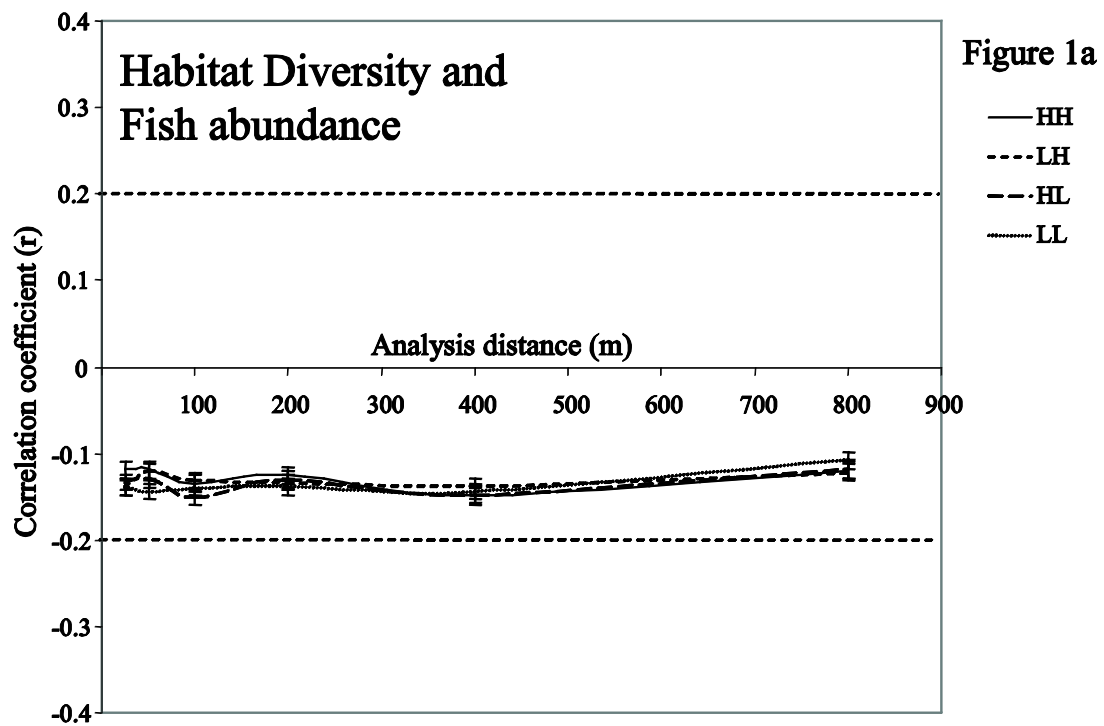
In addition, more map types than the four used here should be considered in future studies. Only two levels of spatial and thematic resolution respectively were included. While these were set at commonly used levels in reef ecosystem mapping,

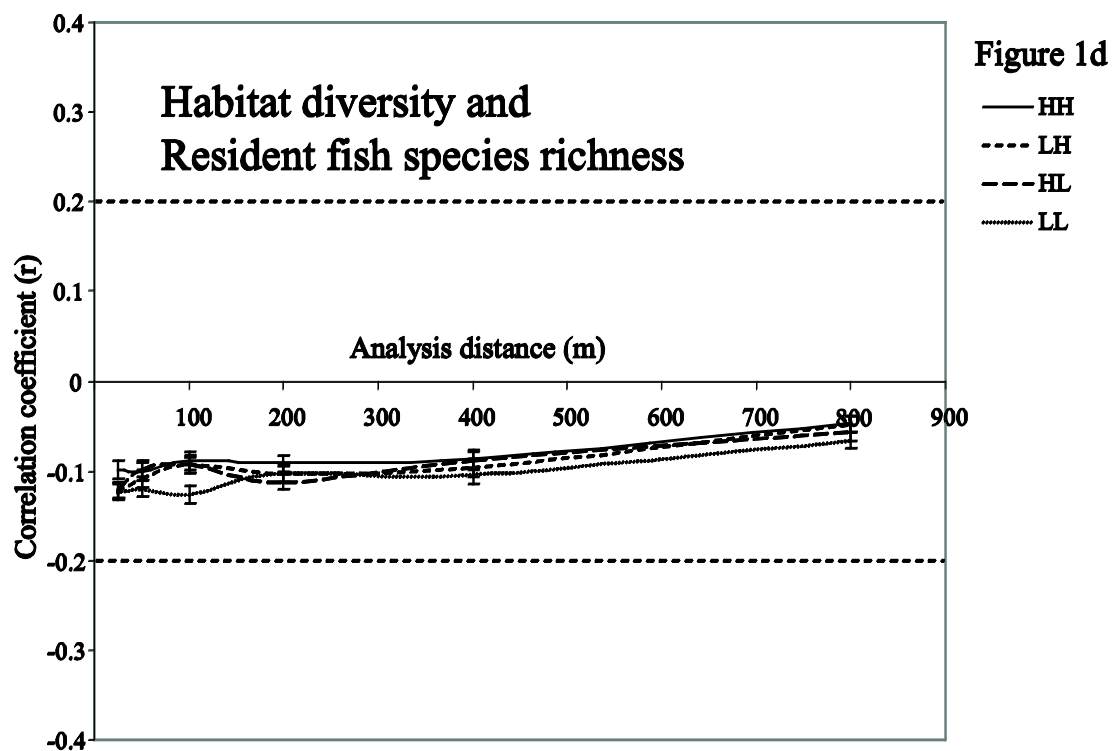
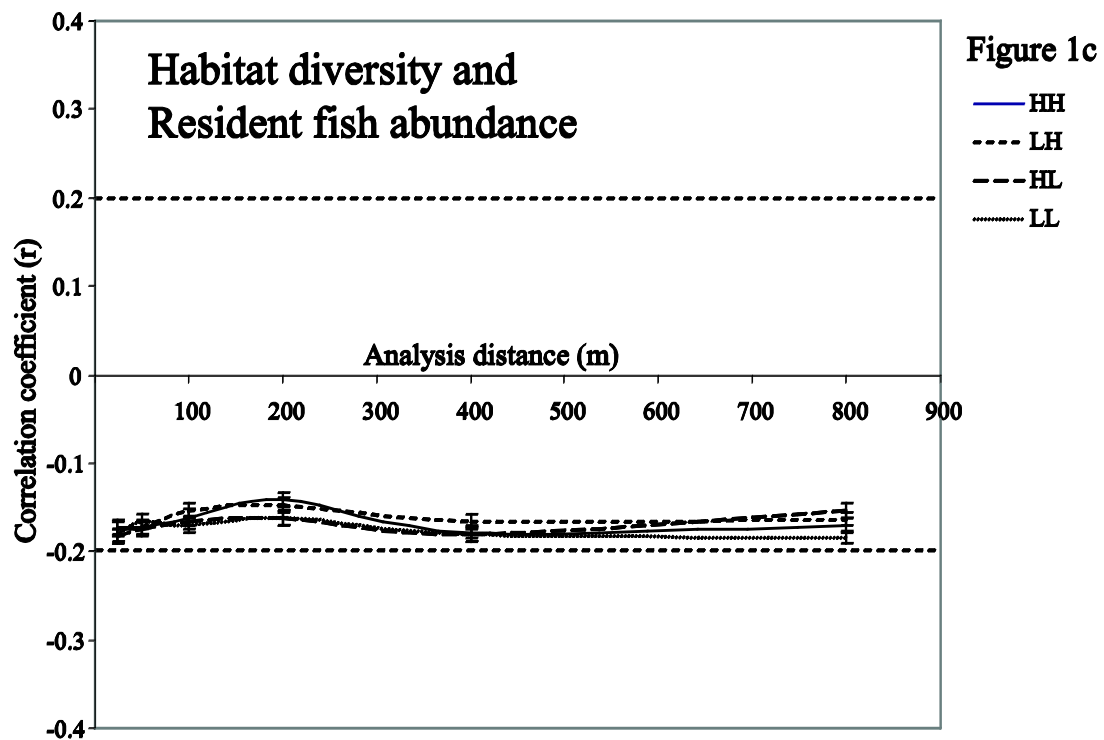
terrestrial studies suggest that some landscape properties vary in non-linear ways when calculated through a range of map resolutions. Similar phenomena are possible for maps of reef ecosystems. Not only that, but completely different map types should also be investigated. Maps used in the dissertation were vector or polygon based and derived from visual interpretation of aerial photography. Grid or raster based maps derived from other technologies such as lidar, sonar, and satellite imagery are likely to have very different spatial characteristics and thematic attributes.

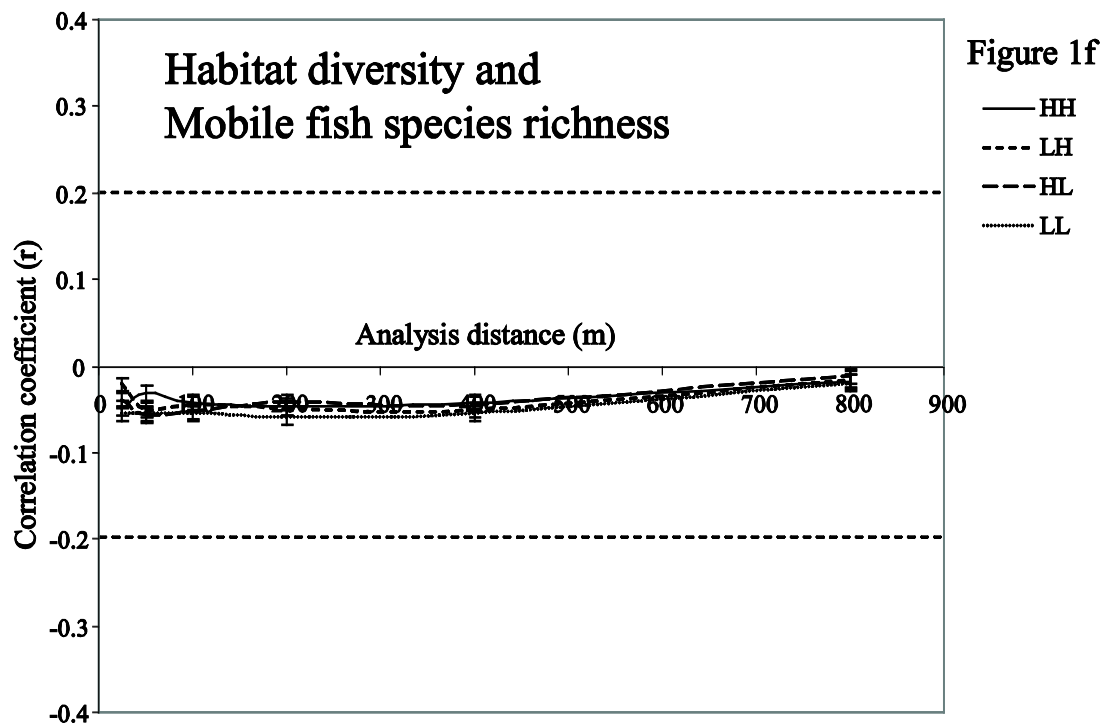
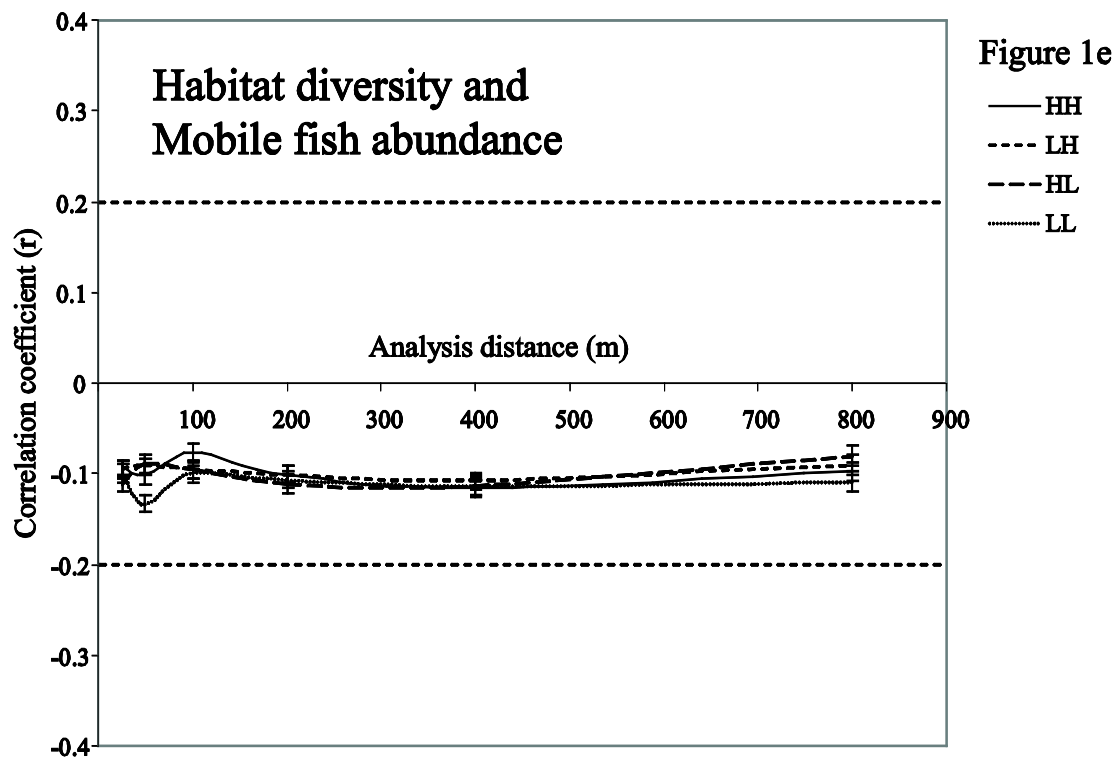
Last, as with many landscape ecological studies, the dissertation is focused on a single landscape. Testing the correlations observed at the BIRNM ecosystem around Caribbean islands with differing geologic history and reef types is needed to put the findings for Caribbean species into a wider geographic perspective. In addition, the BIRNM ecosystem has been heavily altered in the last several decades due to diseases, storms, and anthropogenic impacts. Ecosystem function and structure has changed in unknown ways from the pristine conditions hundreds of years ago. Care must be taken to ensure that the findings for this altered system are relevant in other less impacted settings. The approaches used here should then be repeated in Pacific and Indian Ocean reef systems to evaluate the scope of the underlying ecological principles uncovered here across the widest diversity of species and geomorphological reef types.

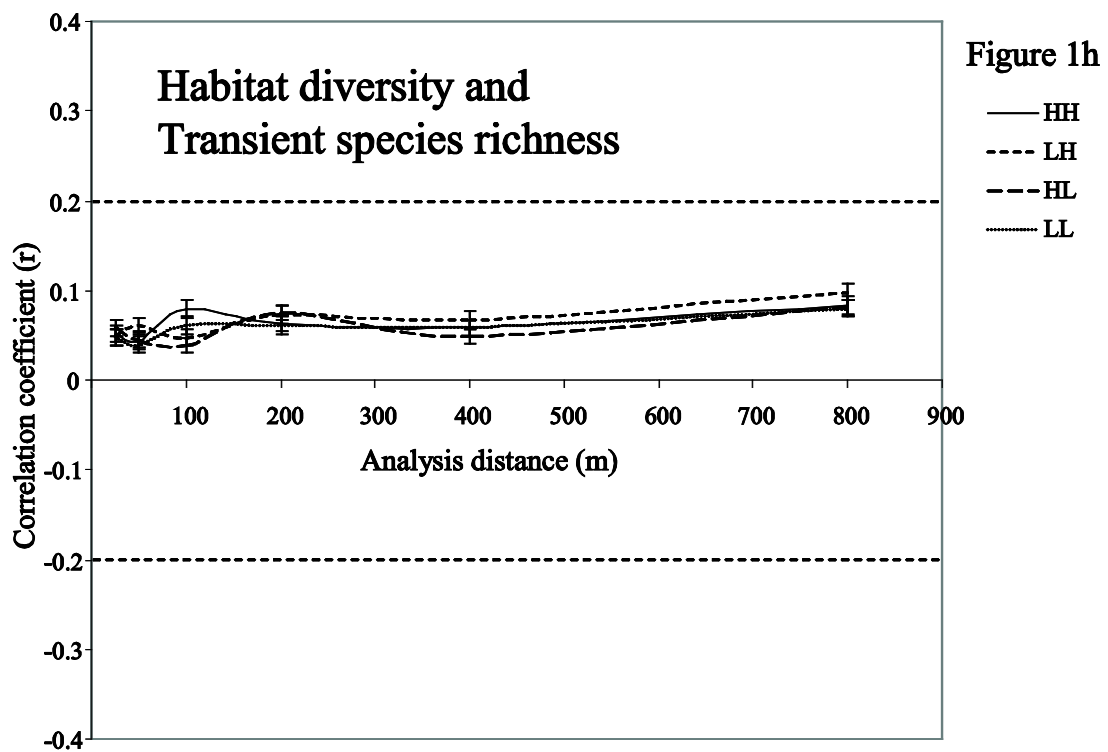
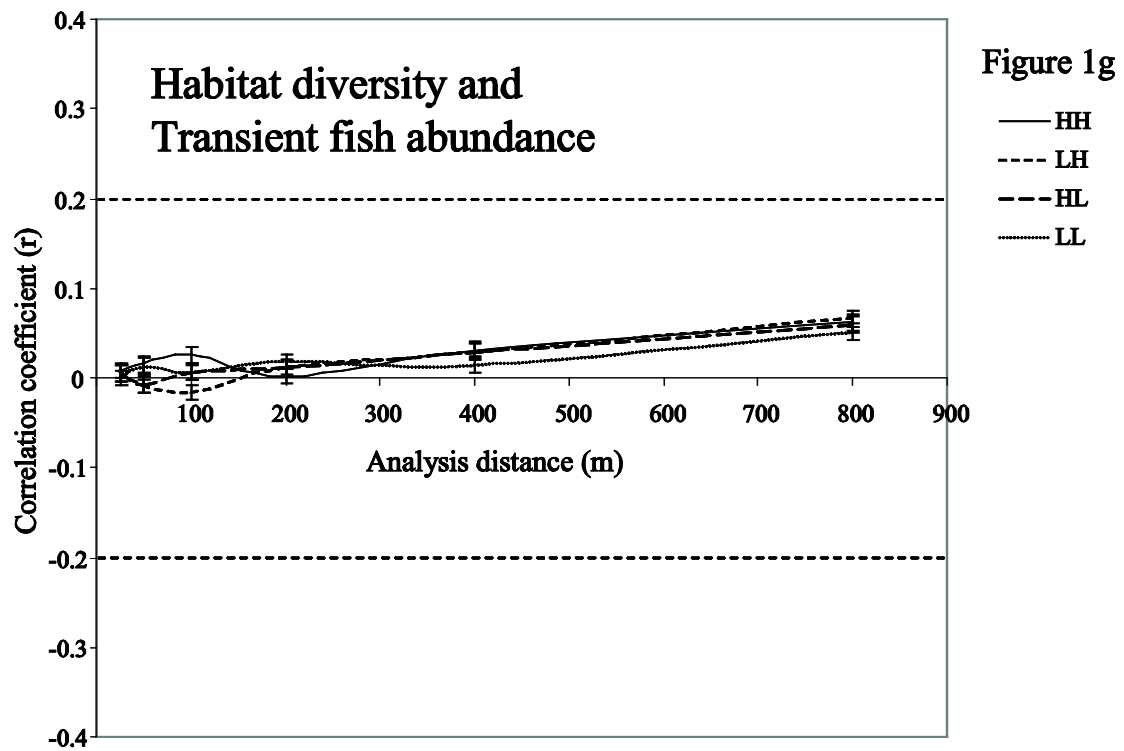
Appendices

Appendix A: Correlation plots of all fish and landscape variables in the study as listed in Table 4.1. Where a significant correlation was found, the vertical lines adjacent to the legend denote map types that have correlations that are not significantly different from each other at the scale with highest correlation. HH denotes high spatial and thematic resolution. HL denotes high spatial, low thematic resolution. LH denotes low spatial, high thematic resolution. LL denotes low spatial and thematic resolution.









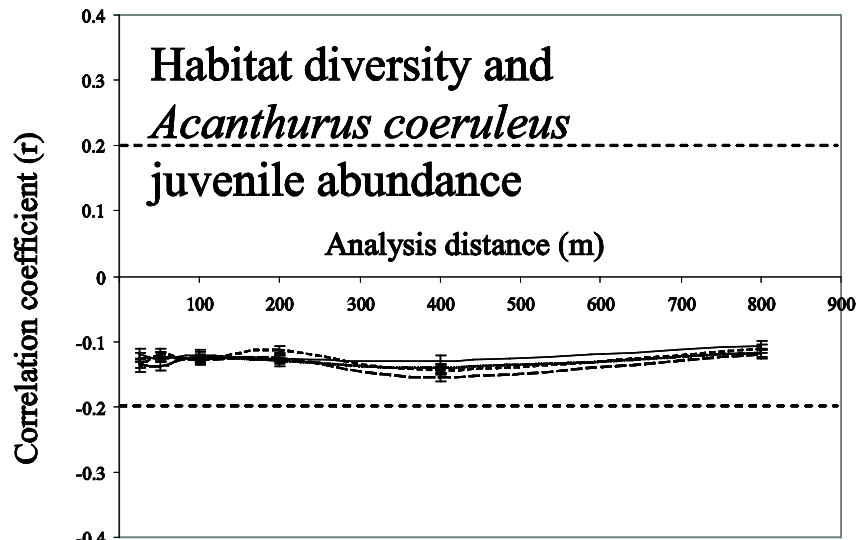


Figure 1i

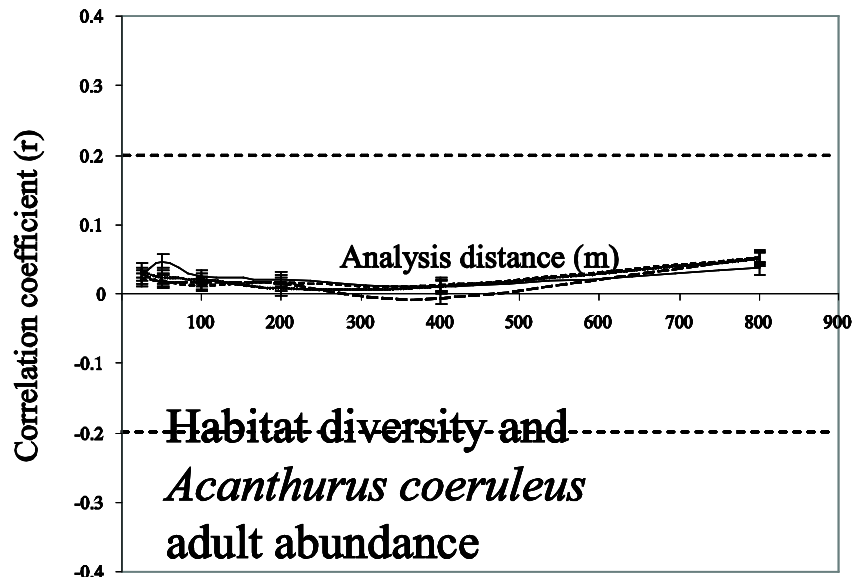


Figure 1j

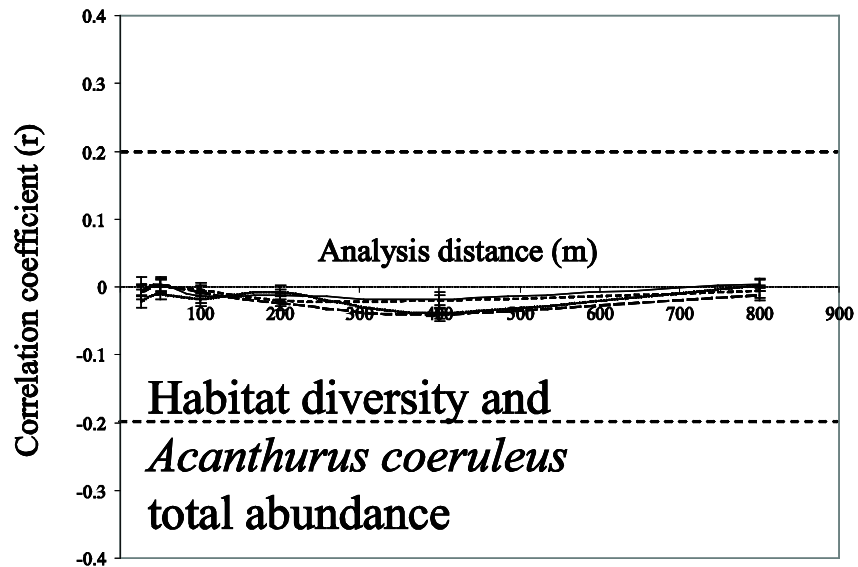


Figure 1k

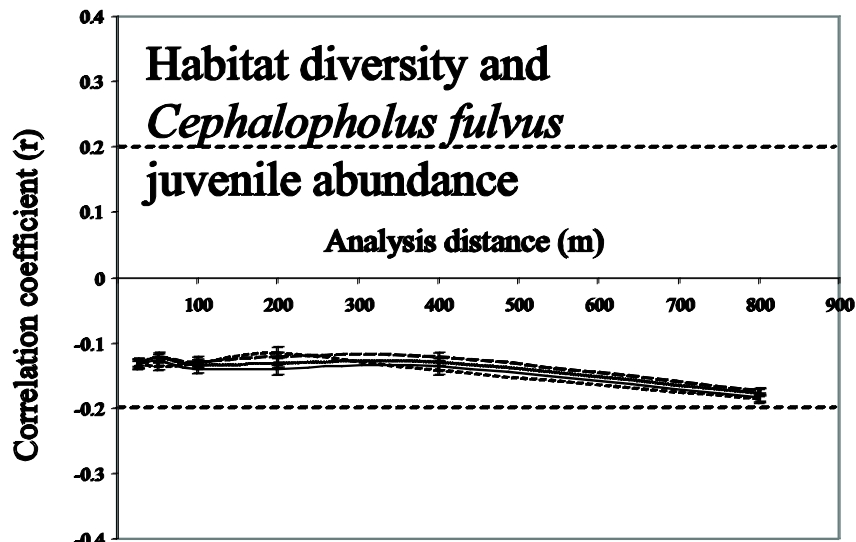


Figure 1l

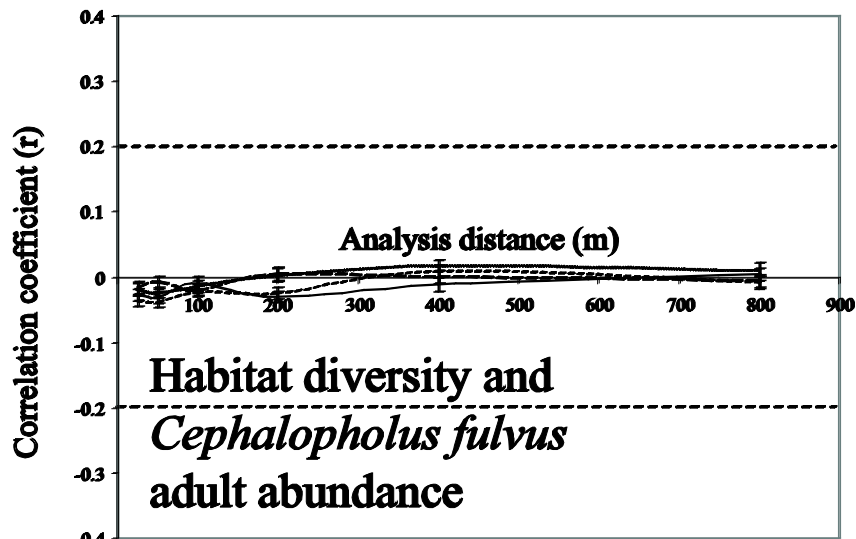


Figure 1m

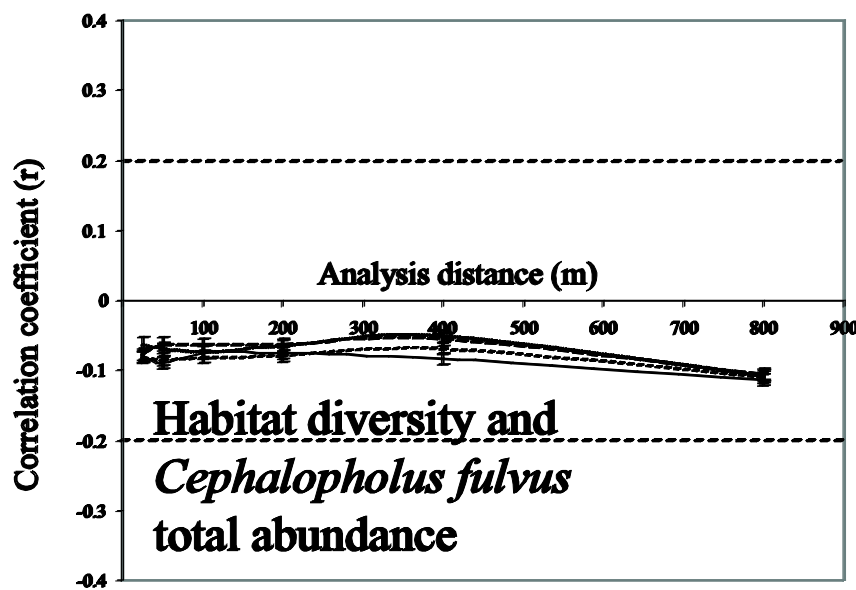


Figure 1n

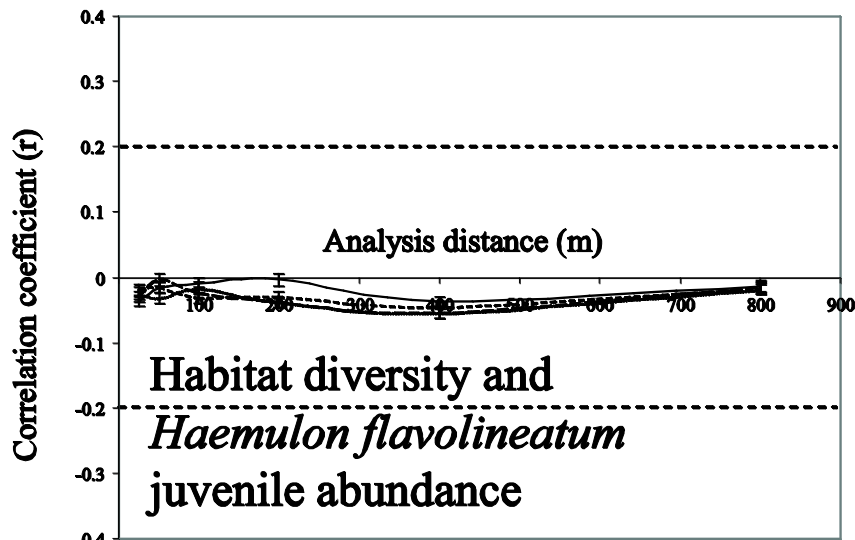


Figure 1o

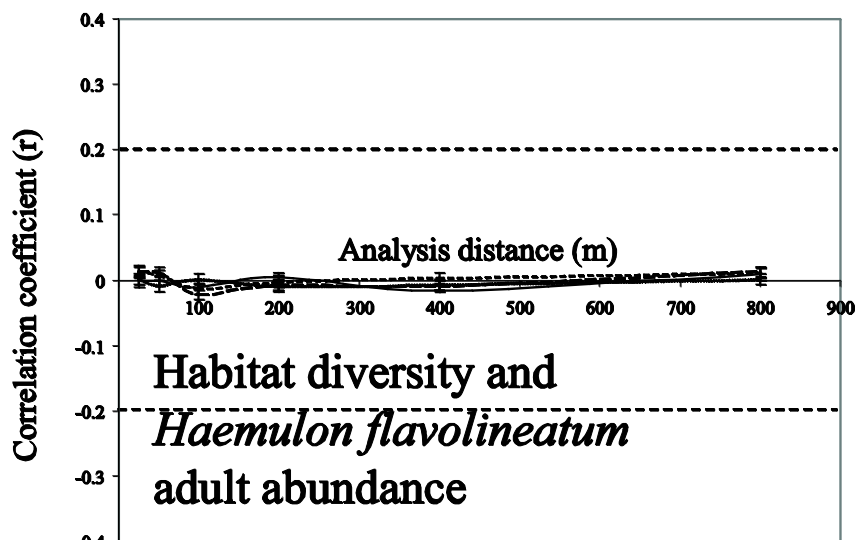


Figure 1p

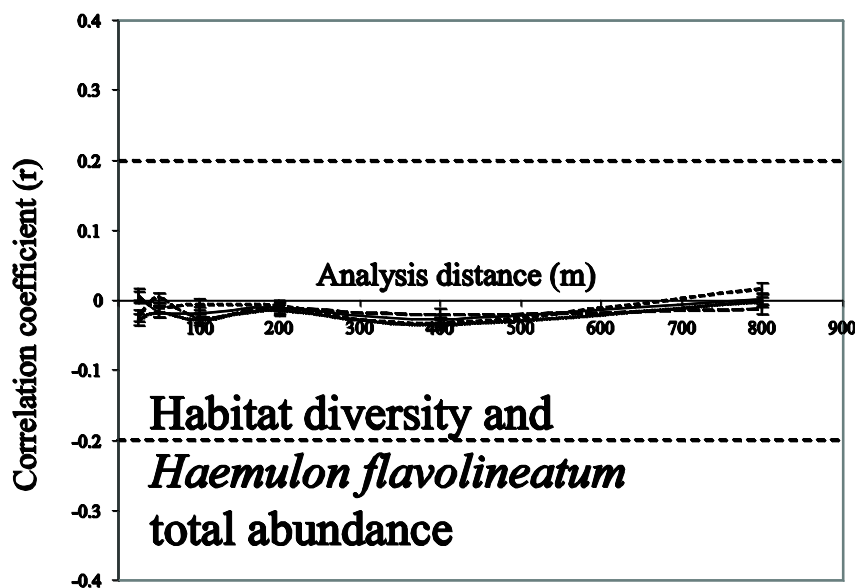


Figure 1q

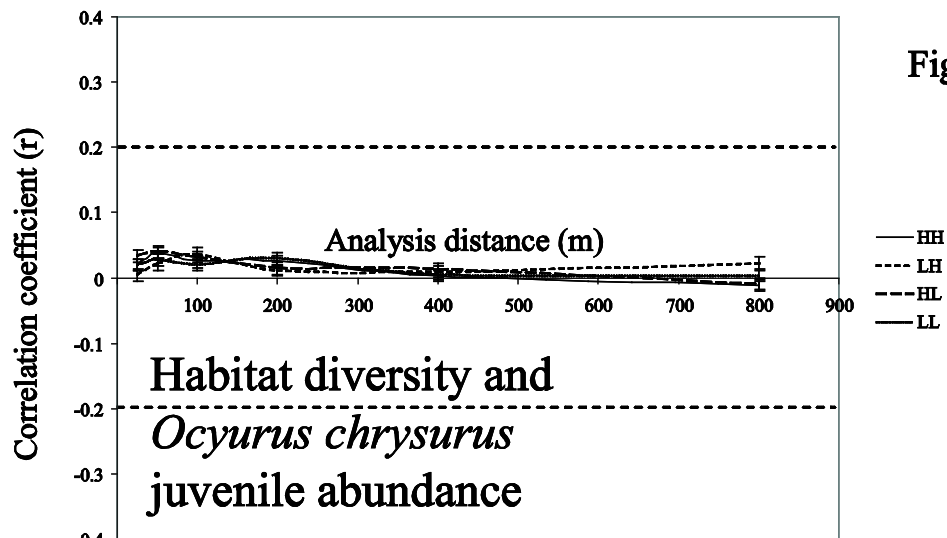


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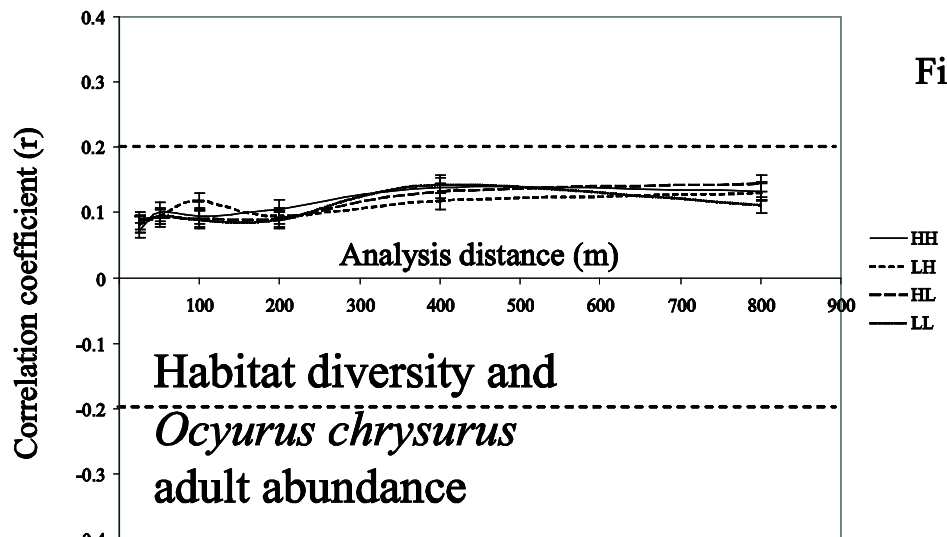


Figure 1s

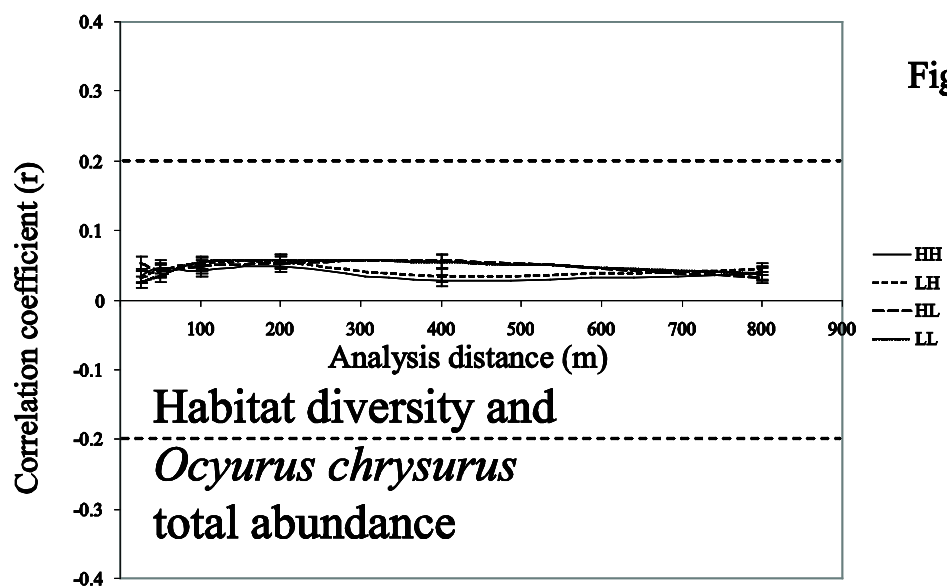


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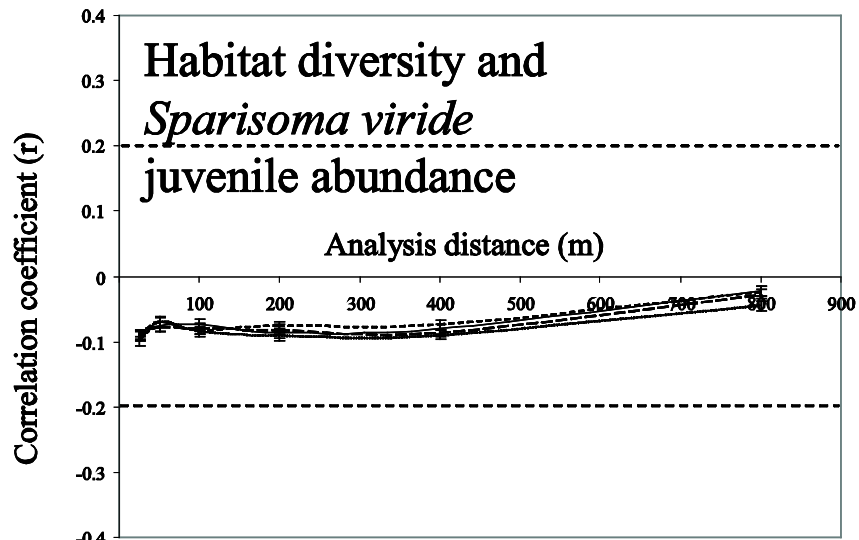


Figure 1u

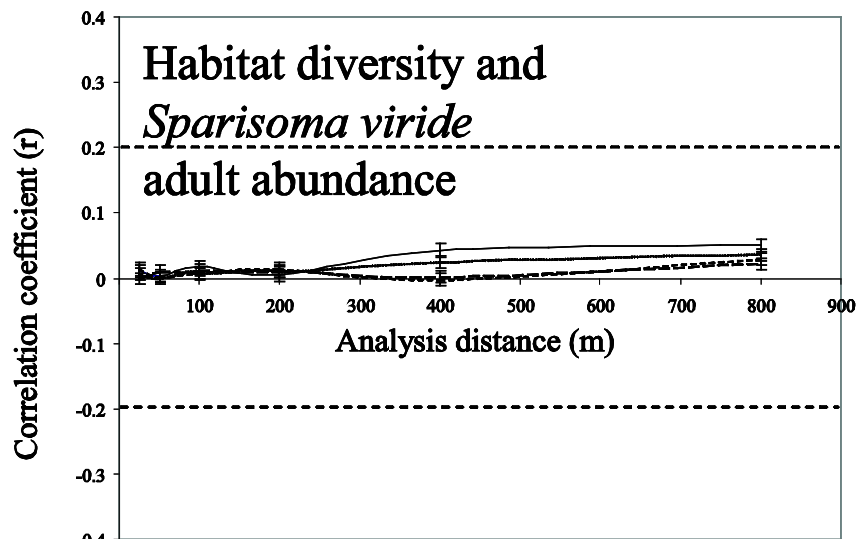


Figure 1v

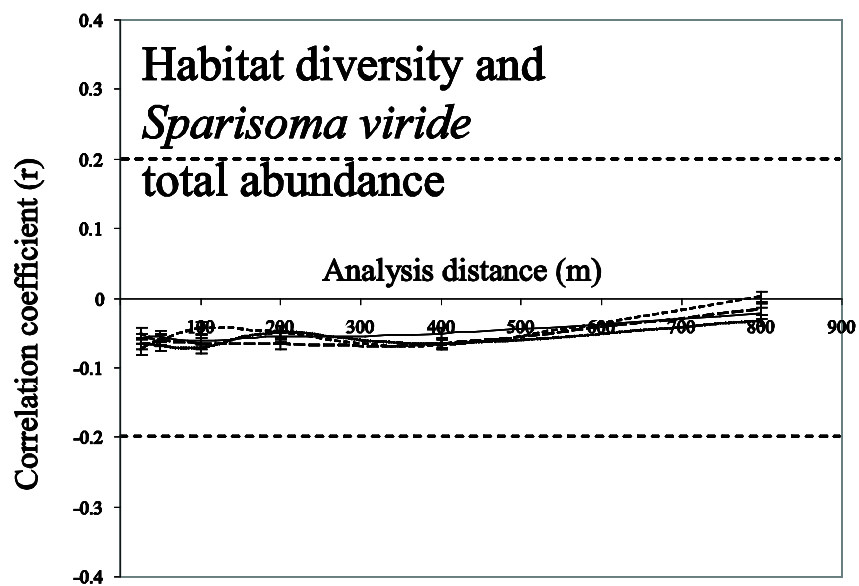


Figure 1w

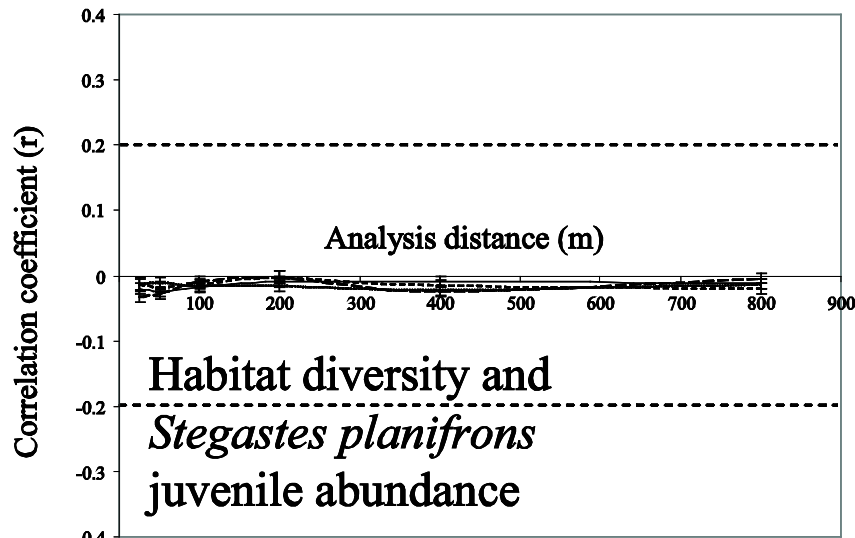


Figure 1x

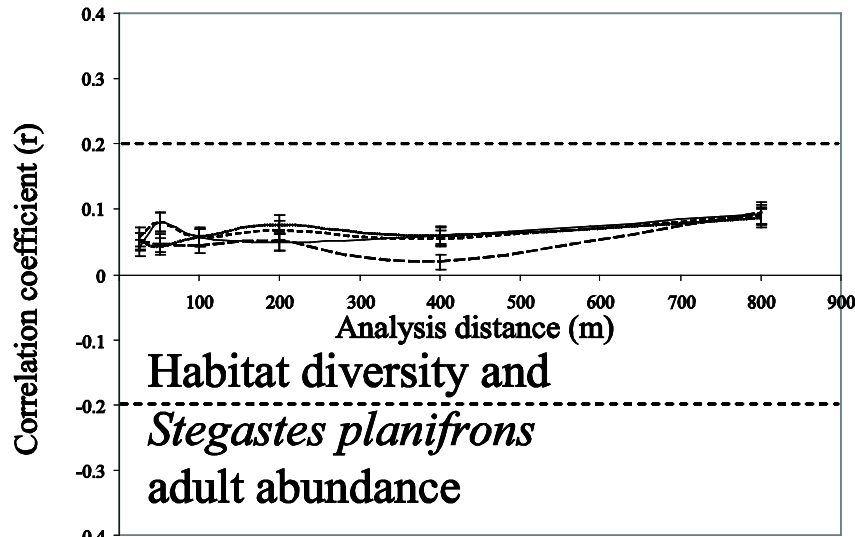


Figure 1y

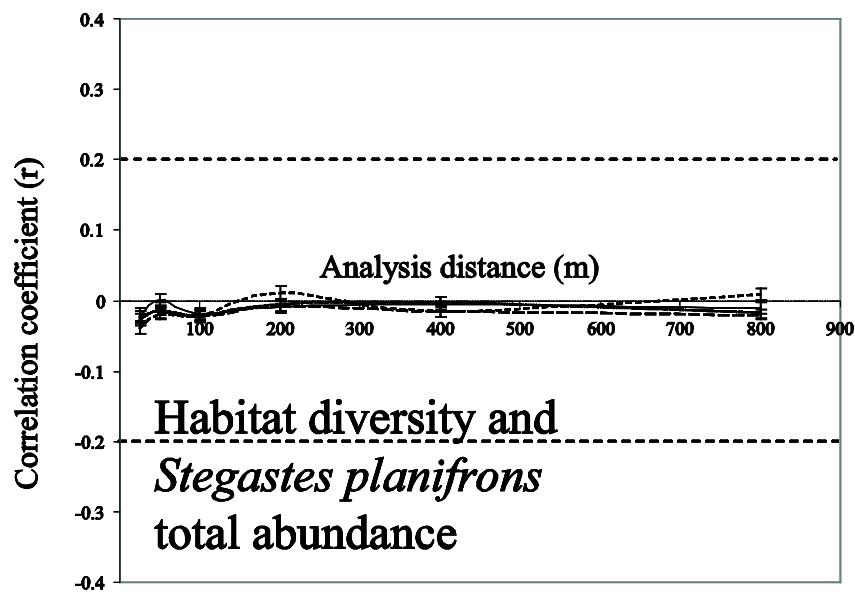


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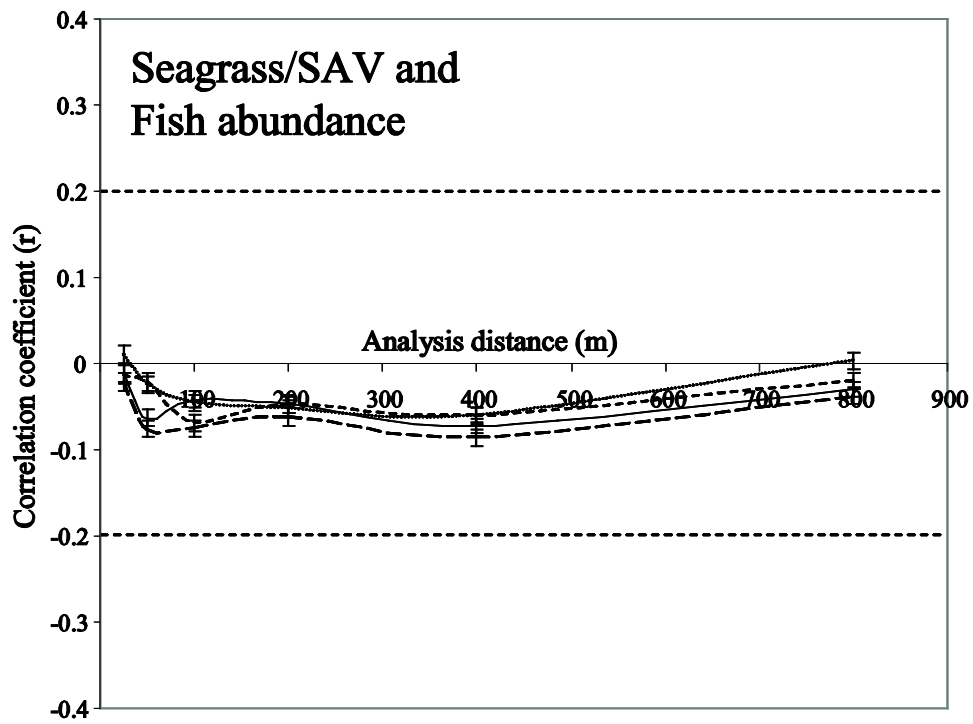


Figure 2a

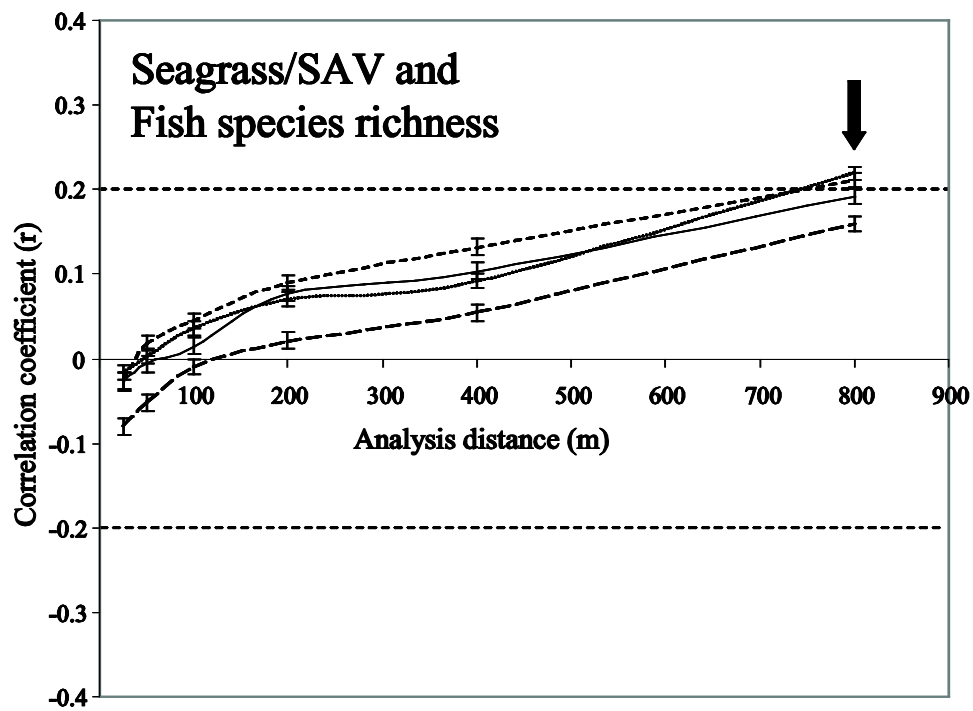


Figure 2b

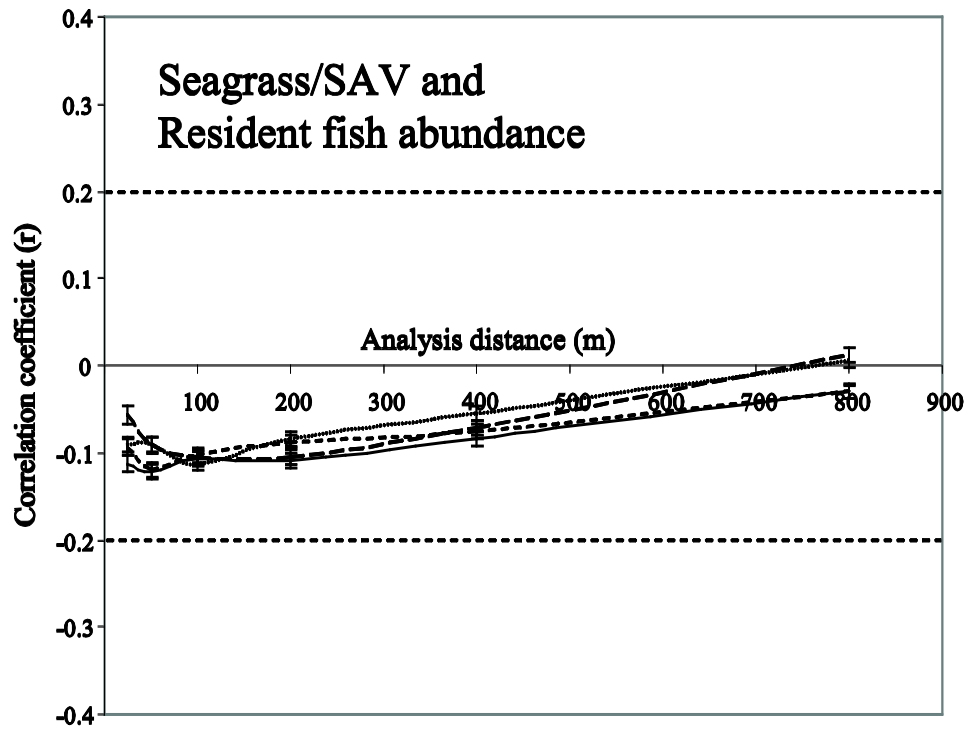


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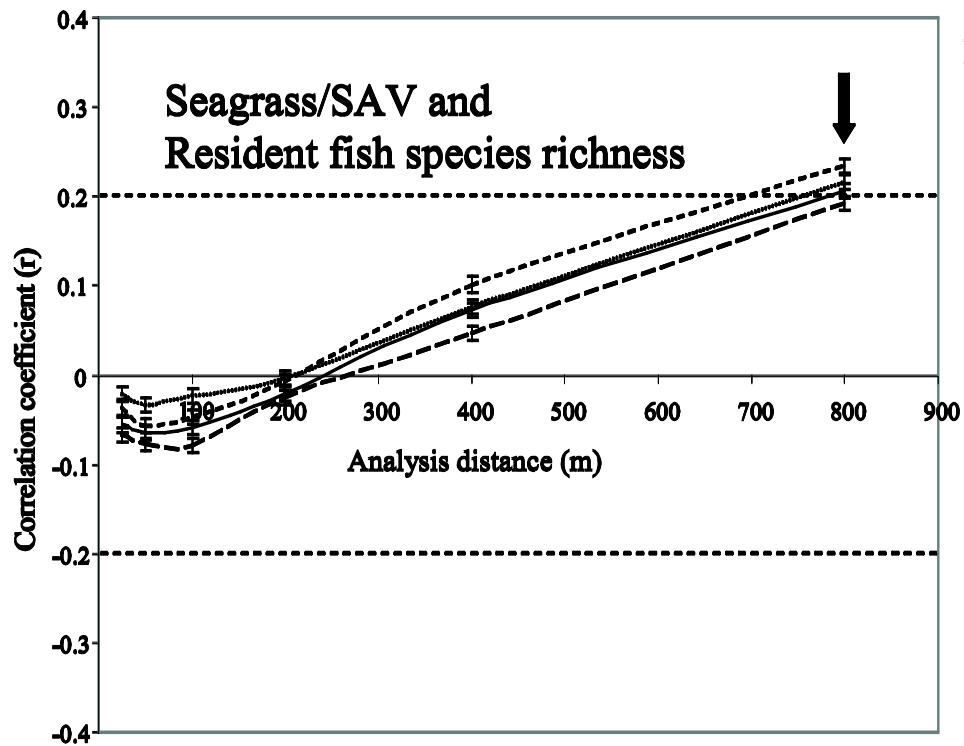
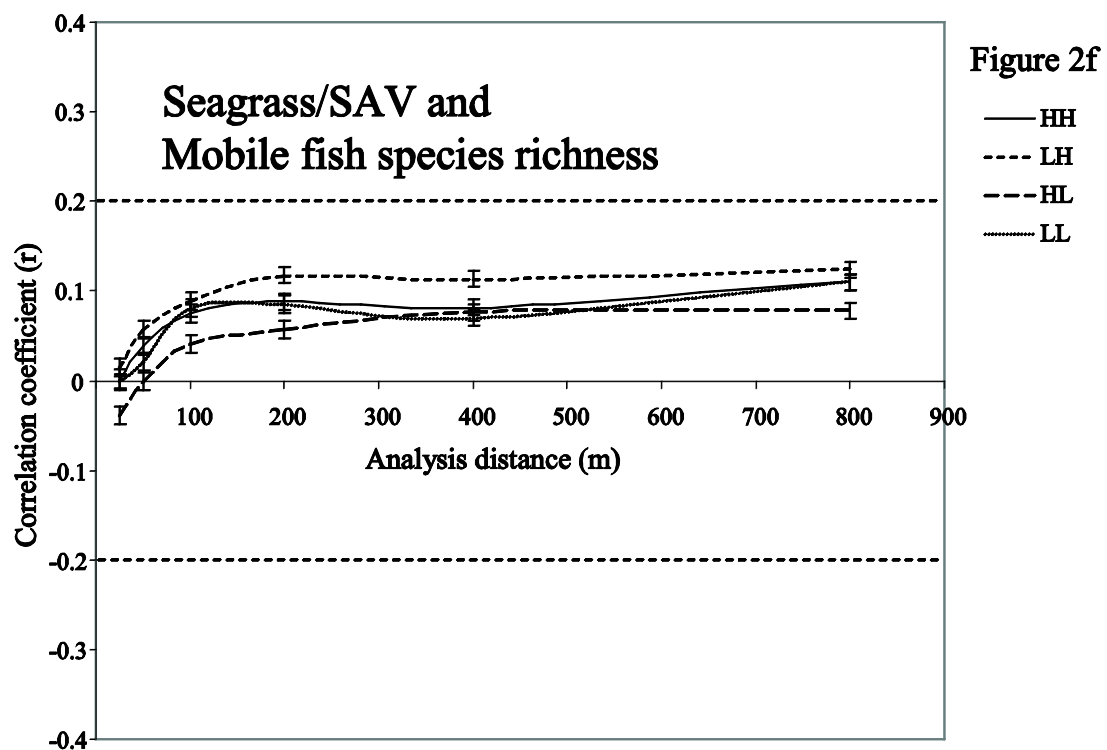
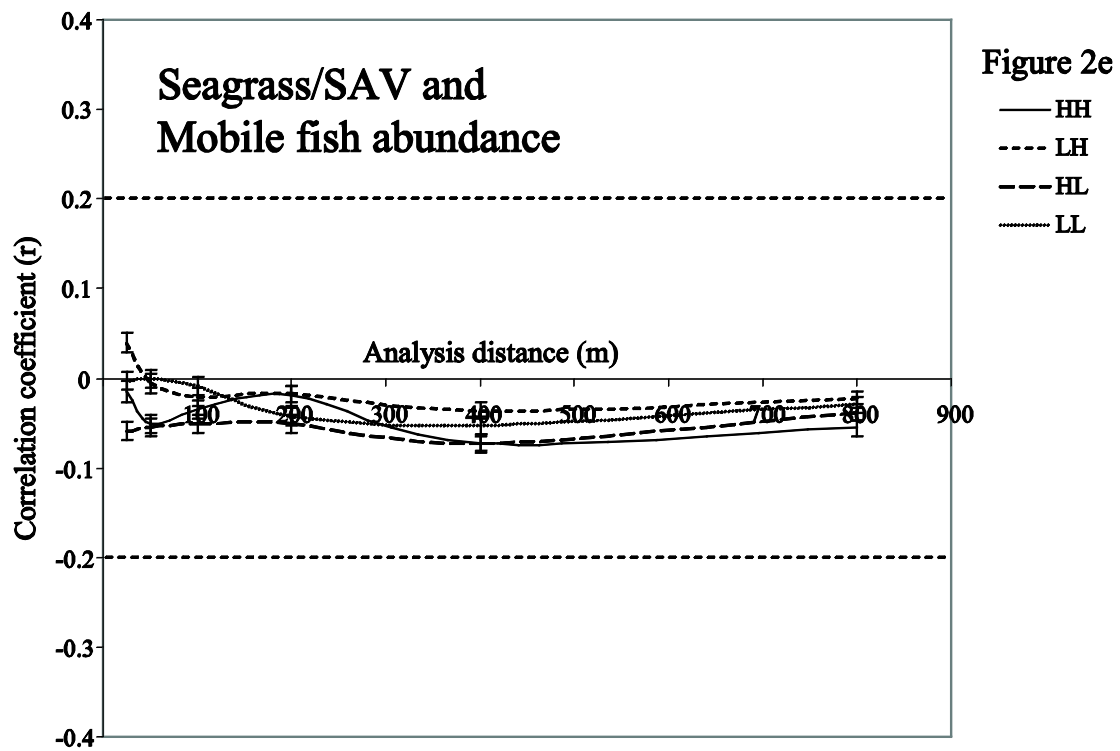
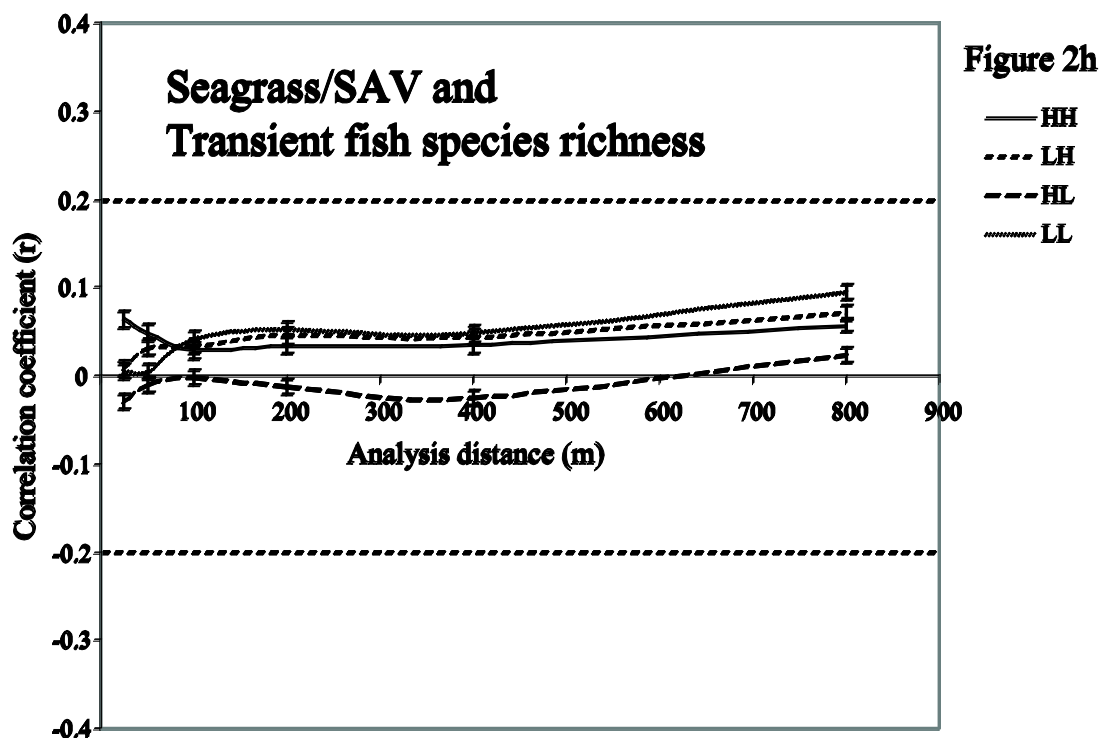
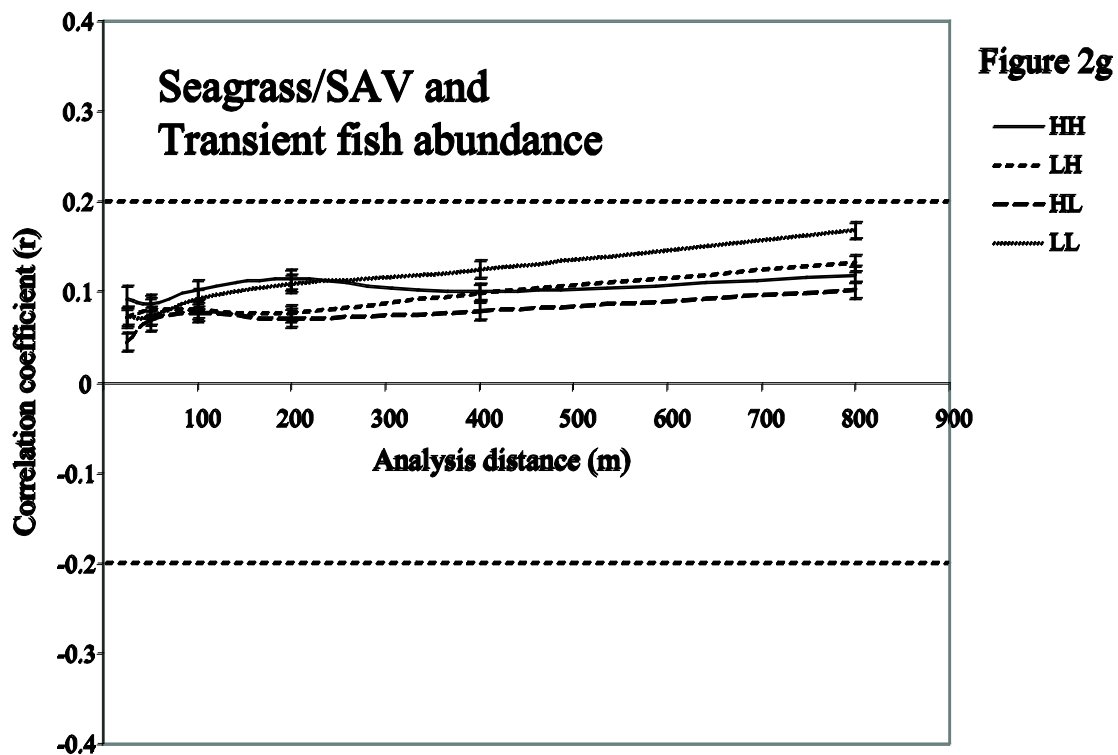


Figure 2d





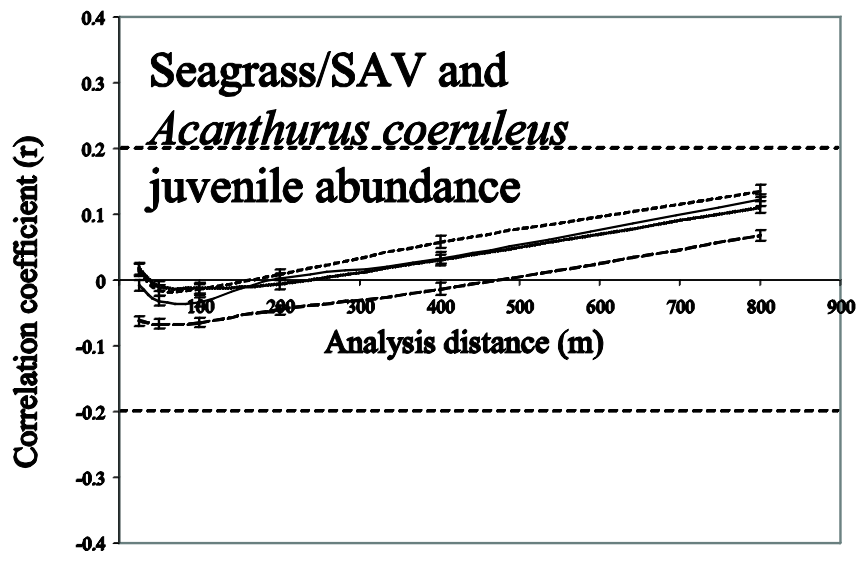


Figure 2i

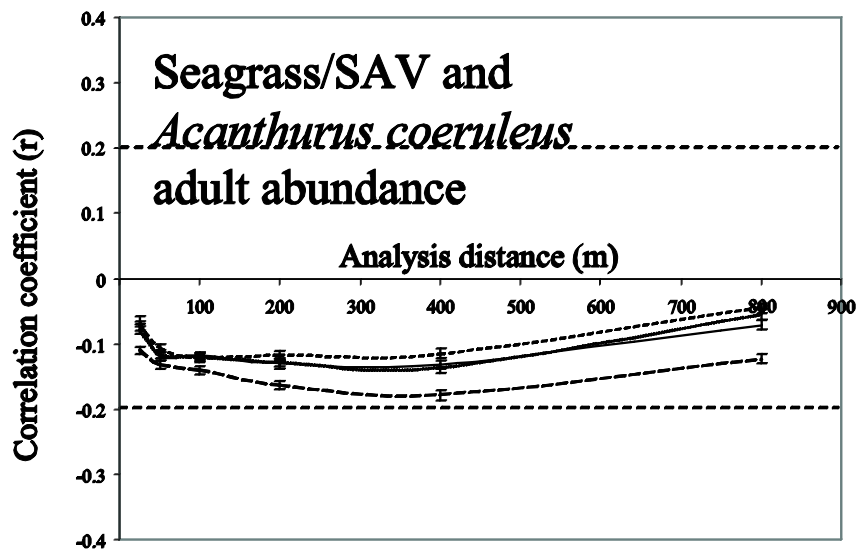


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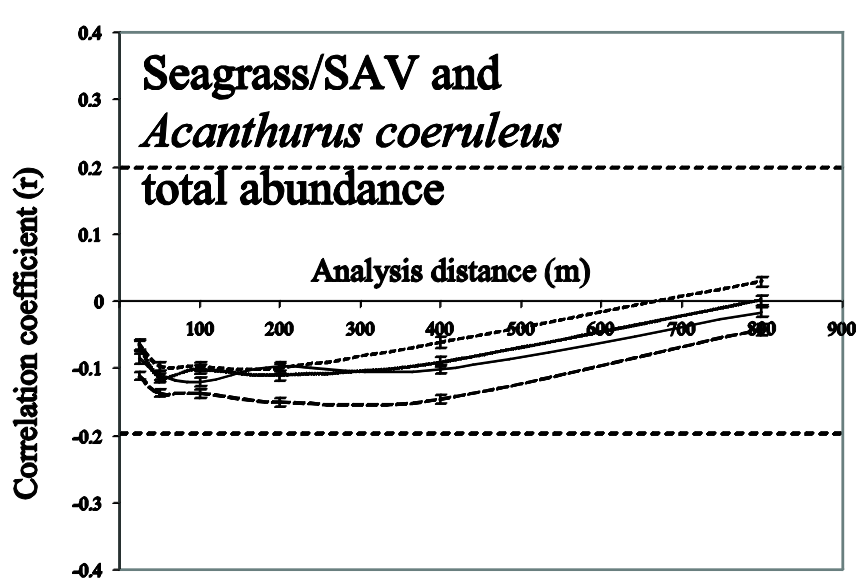


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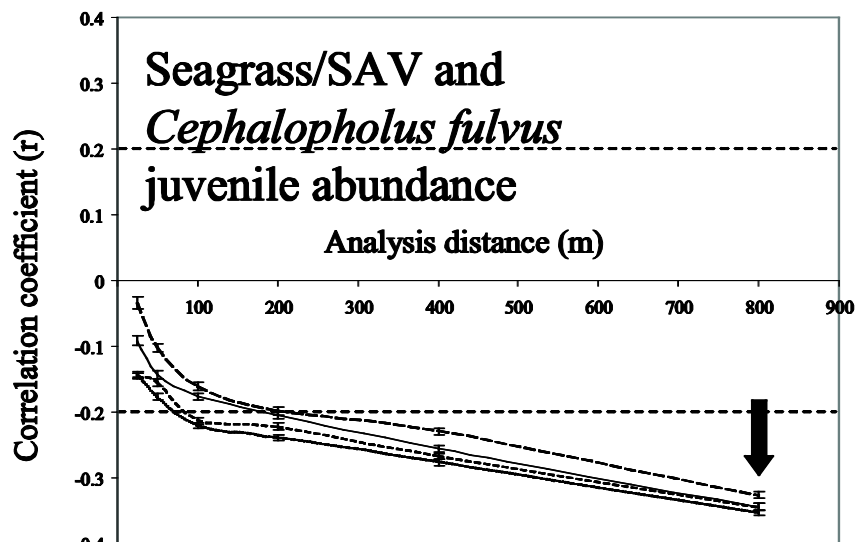


Figure 2l

ANOVA
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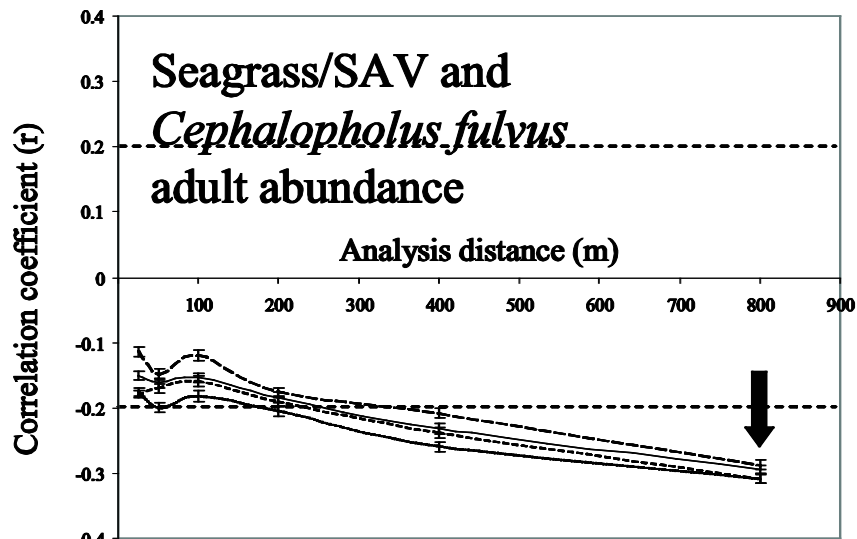


Figure 2m

ANOVA
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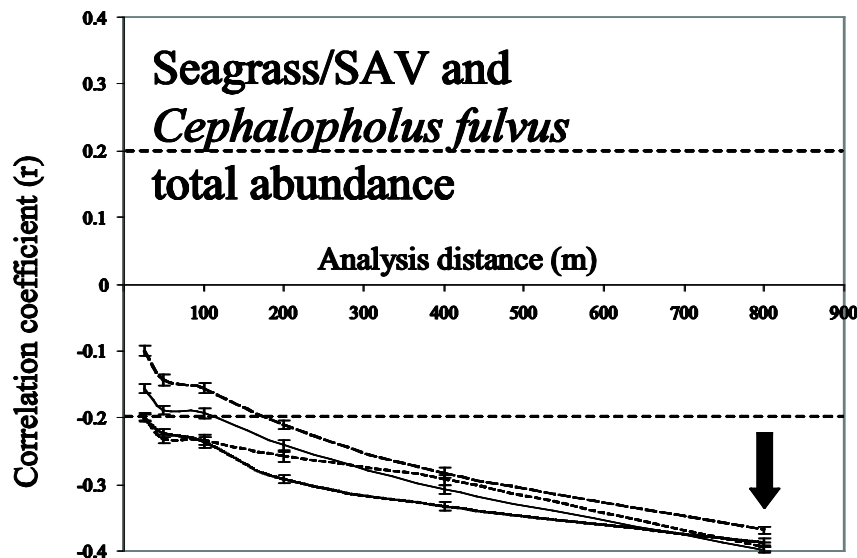


Figure 2n

ANOVA
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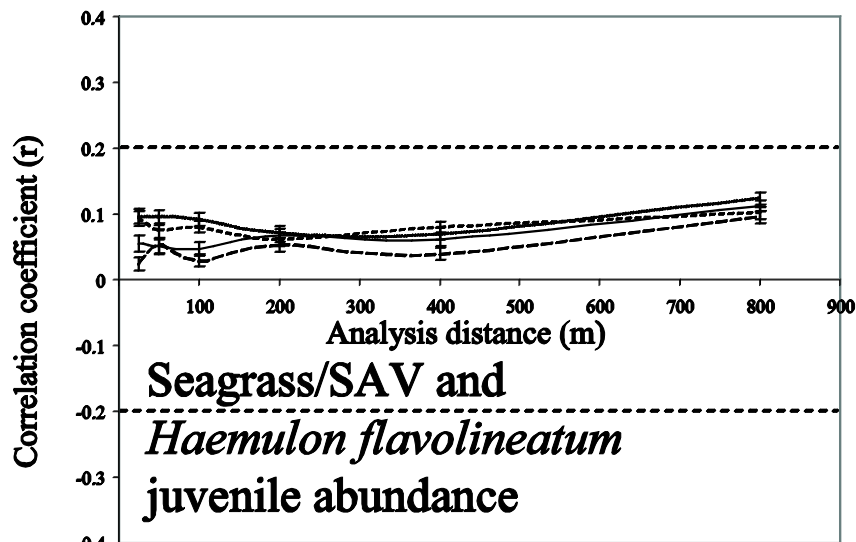


Figure 2o

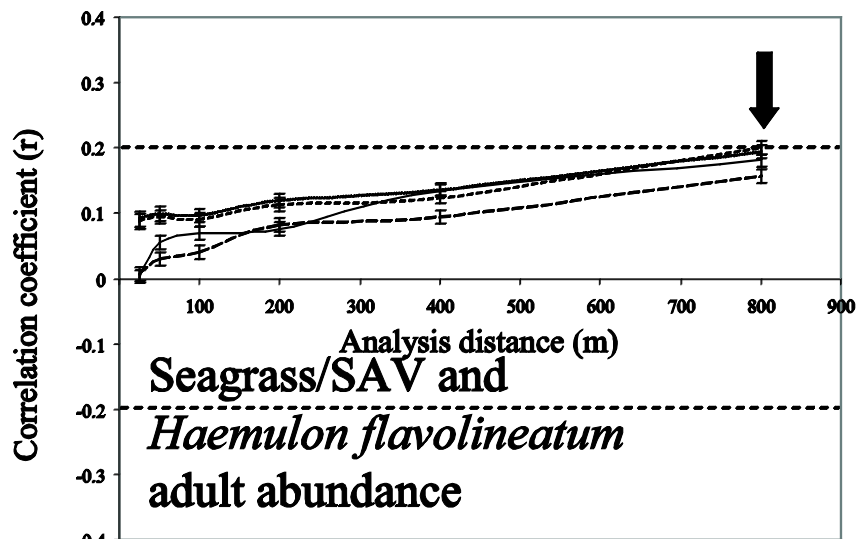


Figure 2p

ANOVA
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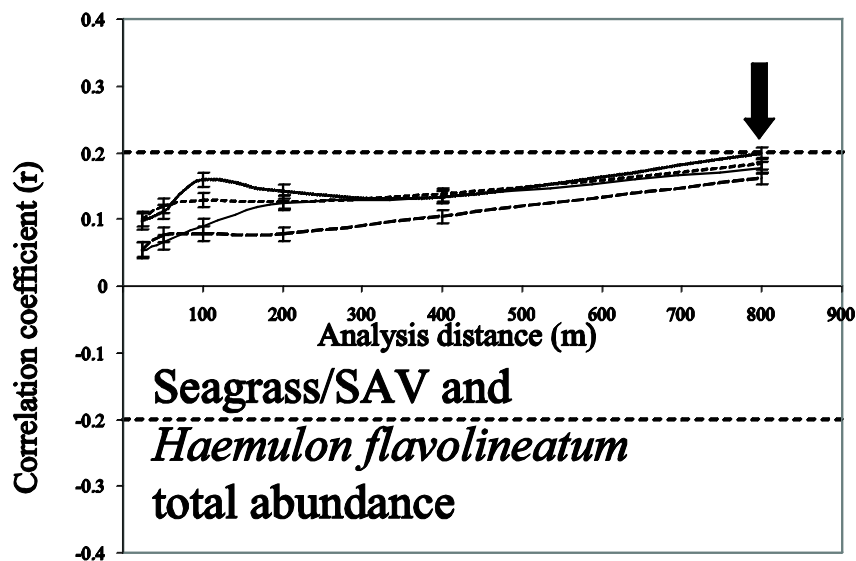


Figure 2q

ANOVA
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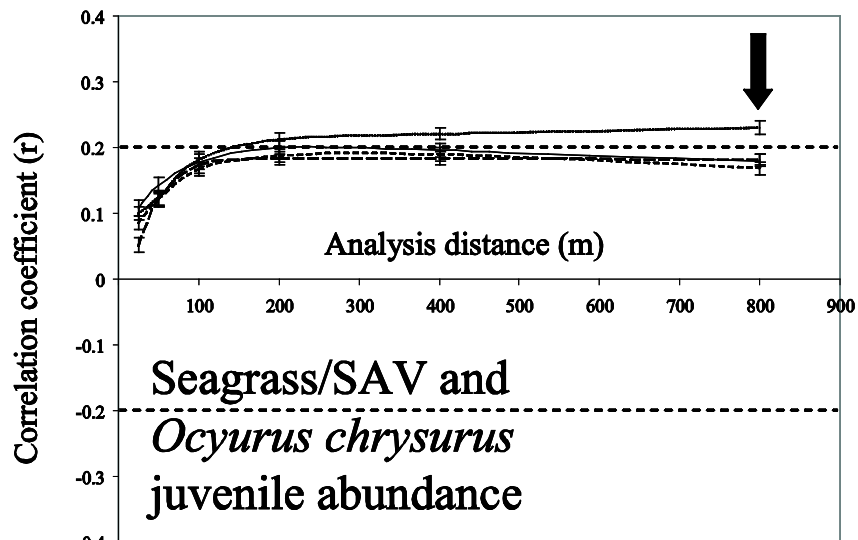


Figure 2r

ANOVA
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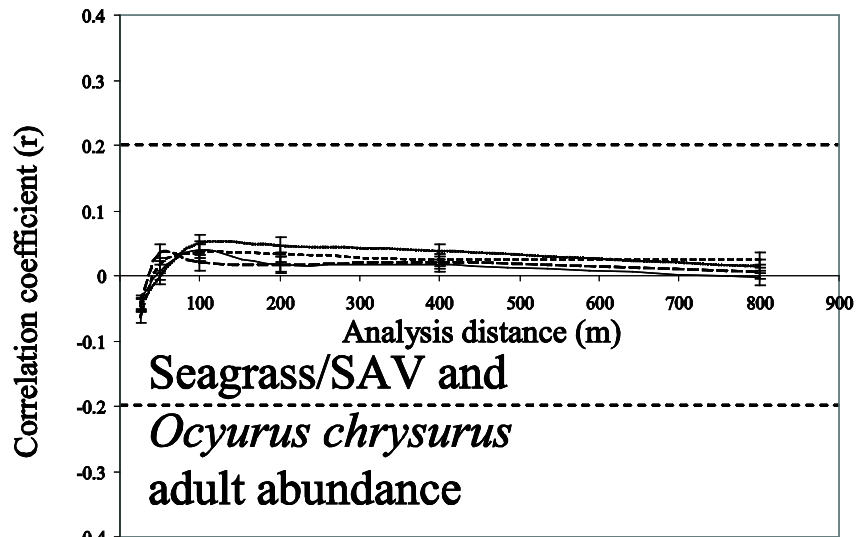


Figure 2s

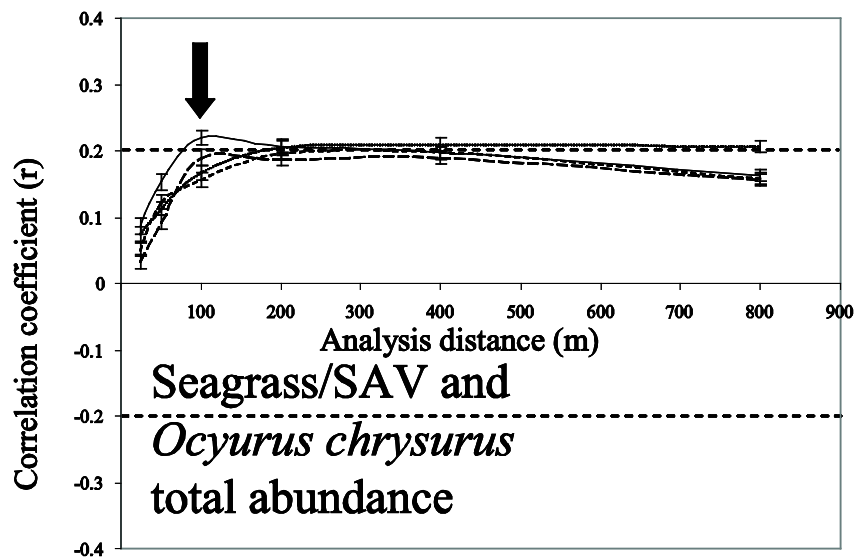


Figure 2t

ANOVA
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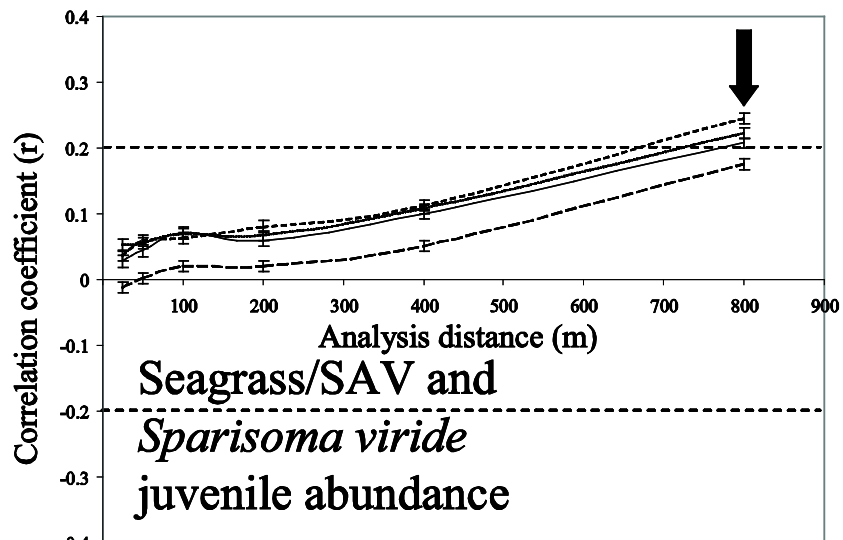


Figure 2u

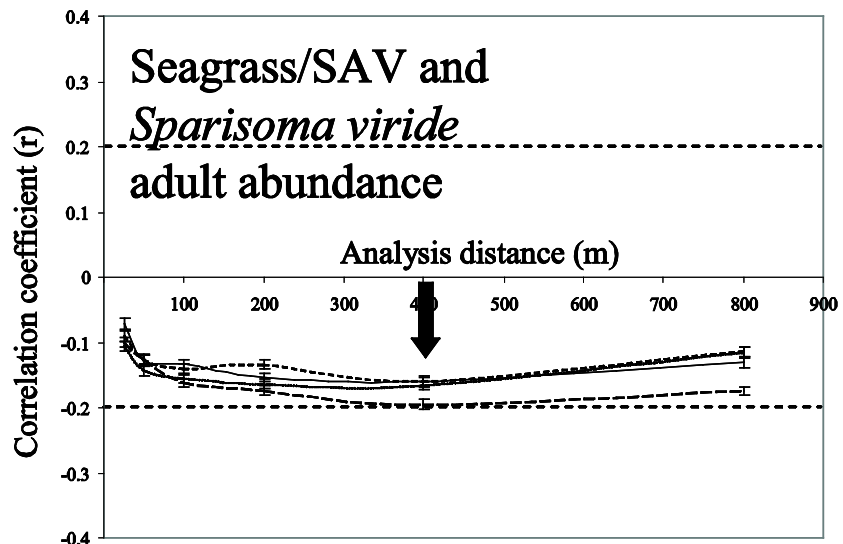


Figure 2v

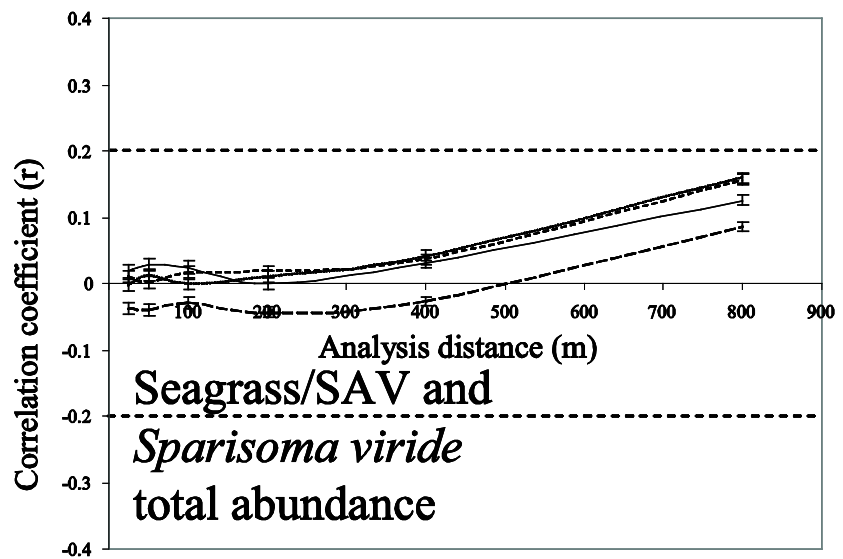


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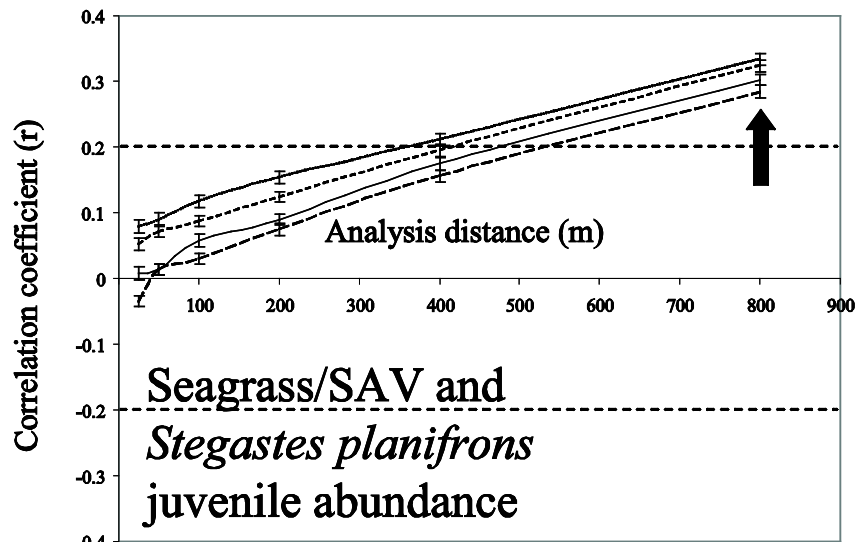


Figure 2x

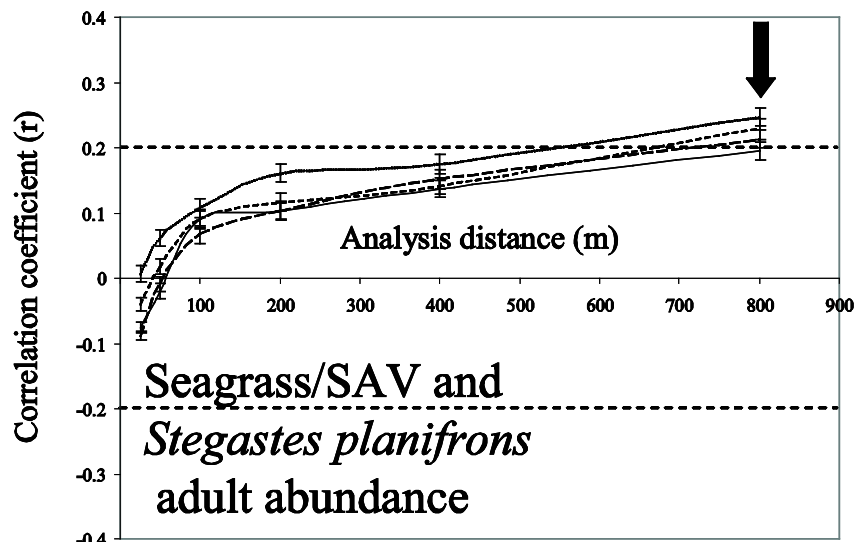


Figure 2y

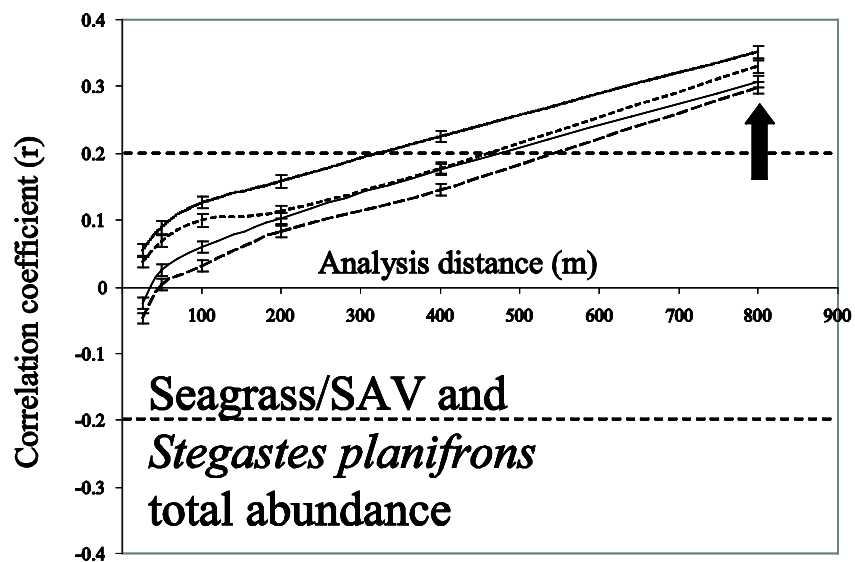


Figure 2z

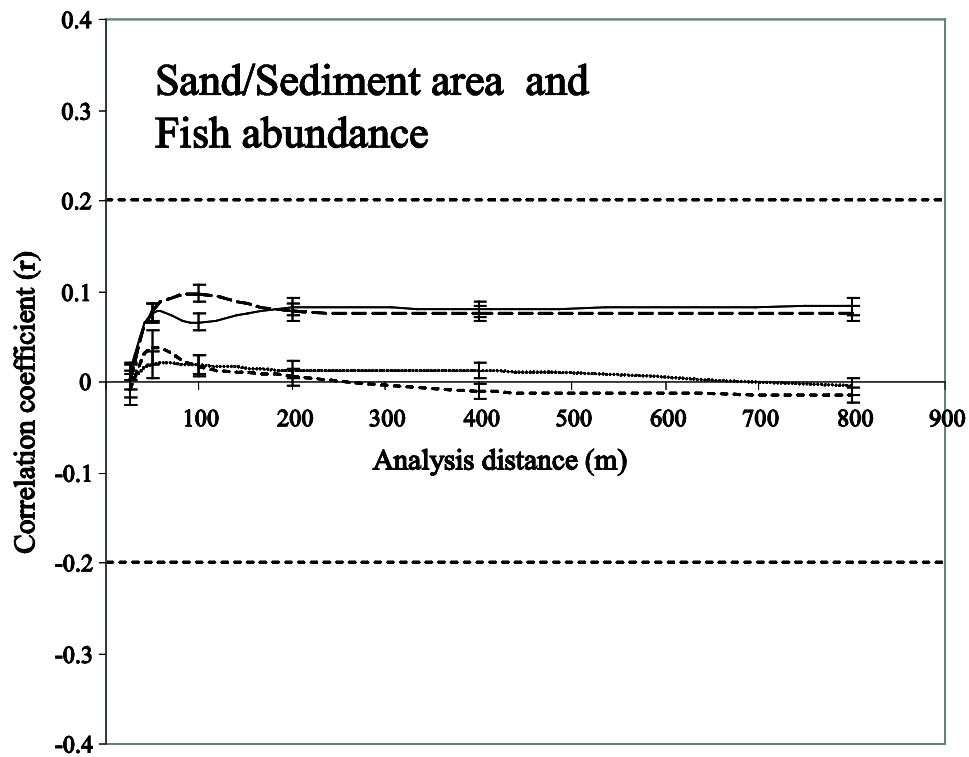


Figure 3a

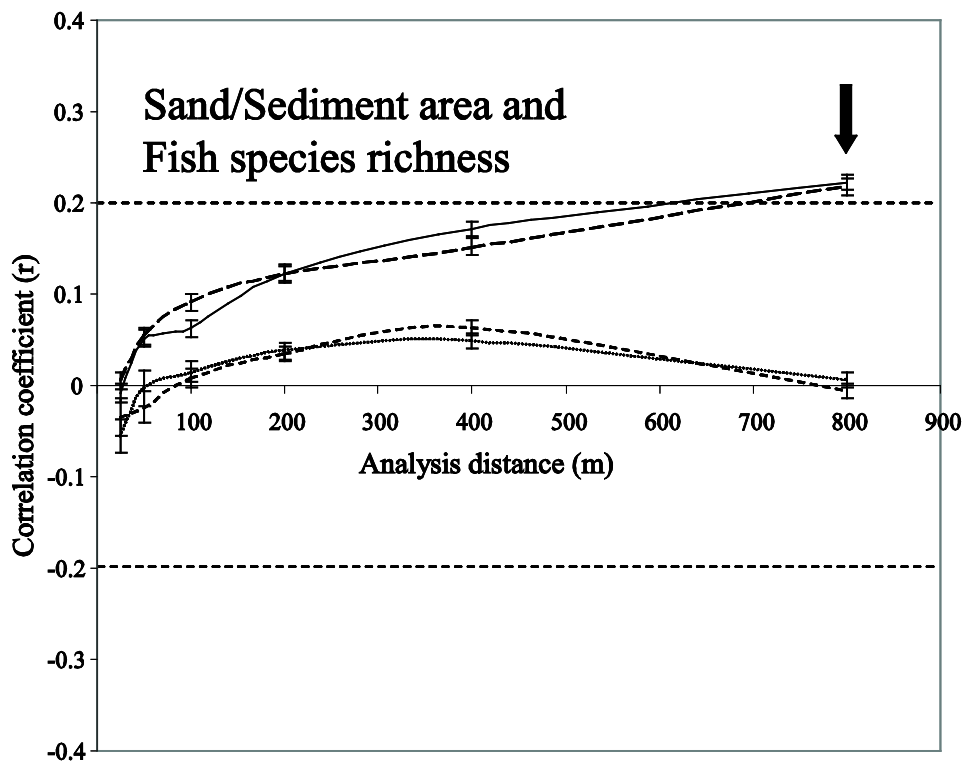
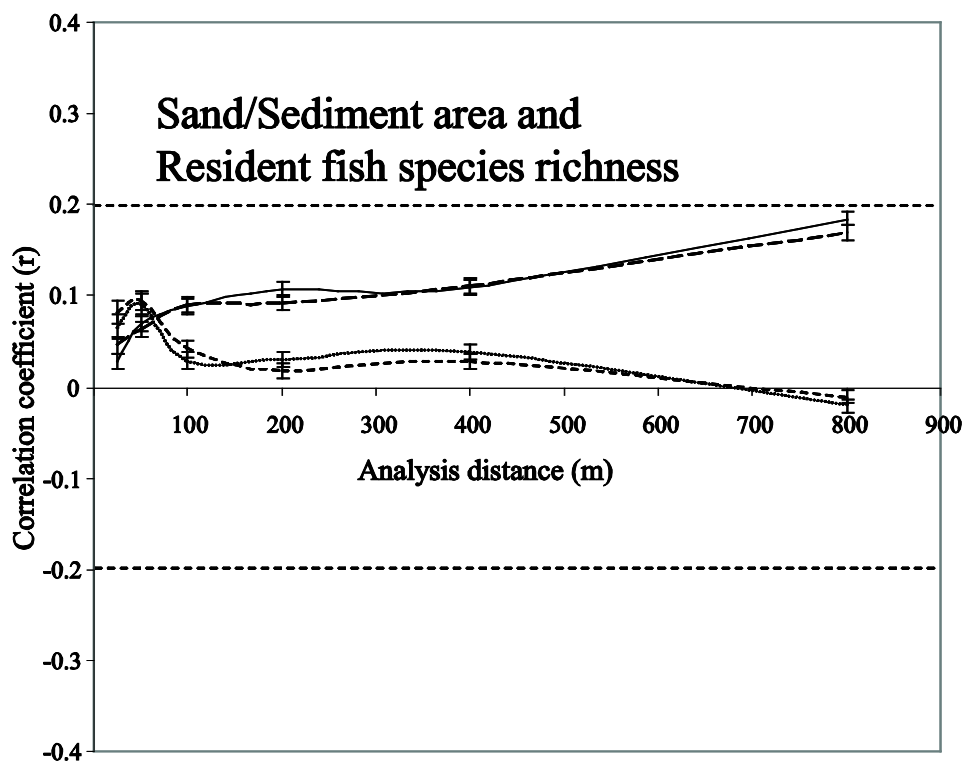
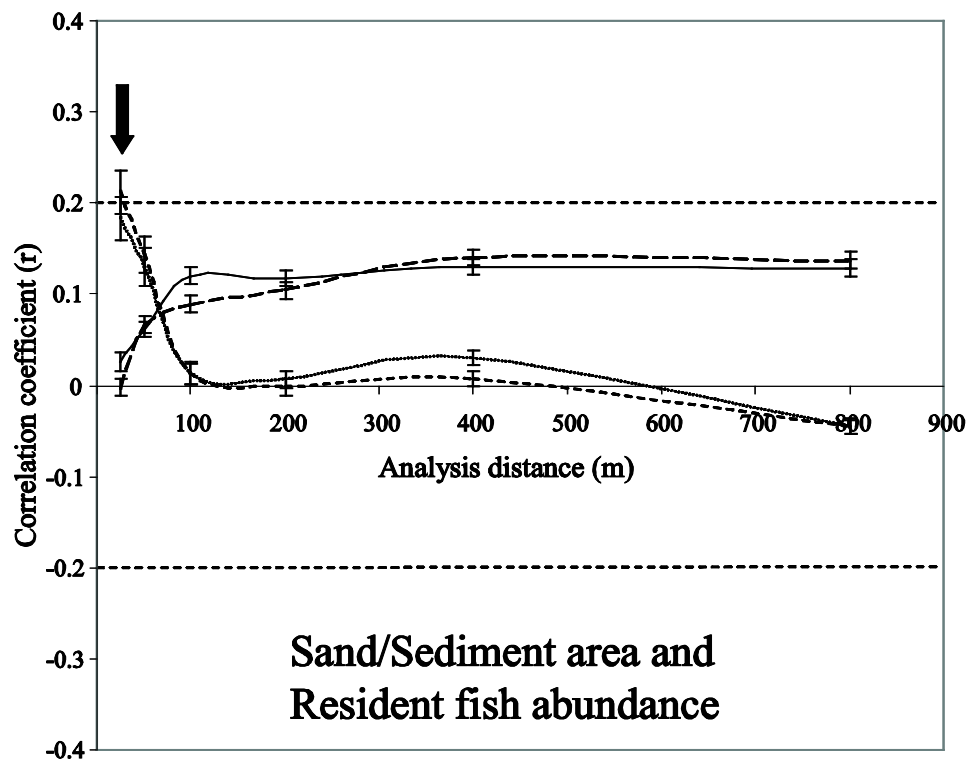
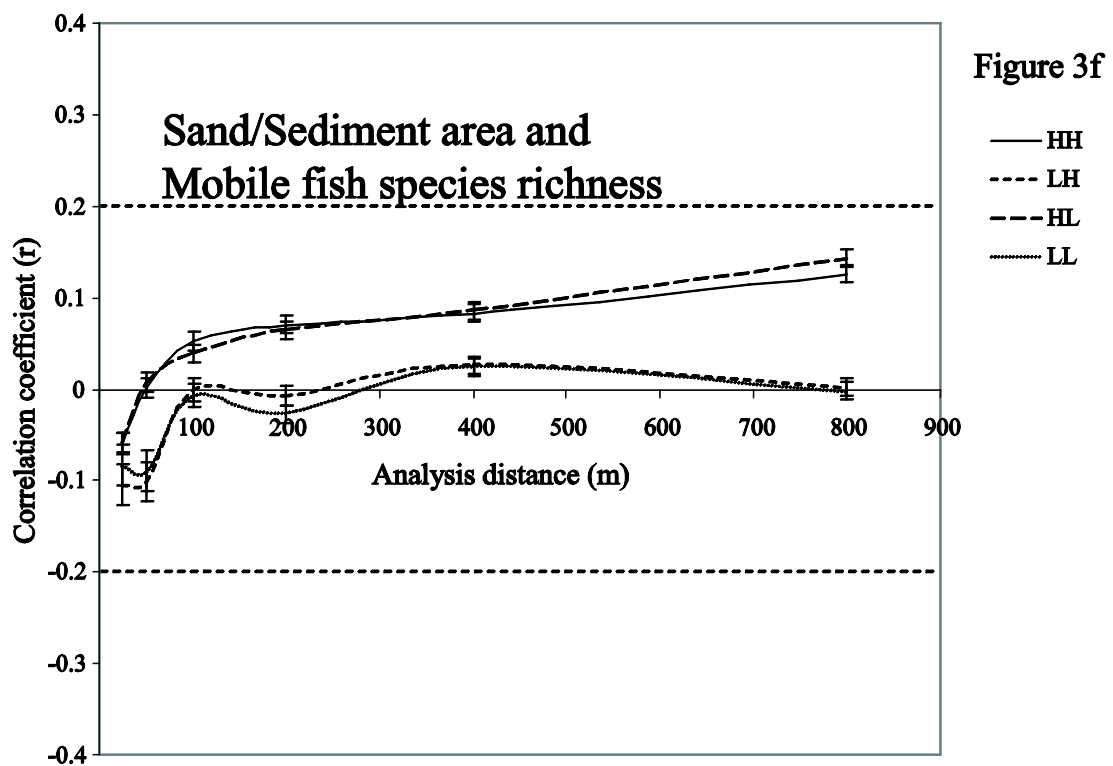
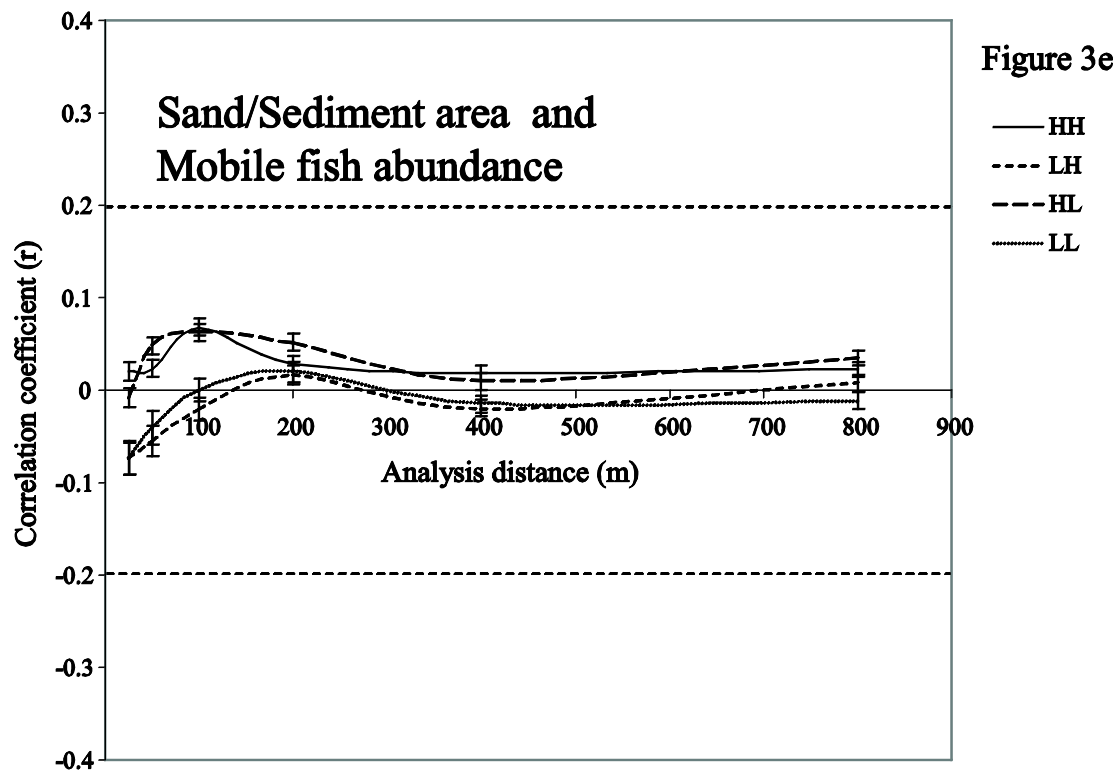
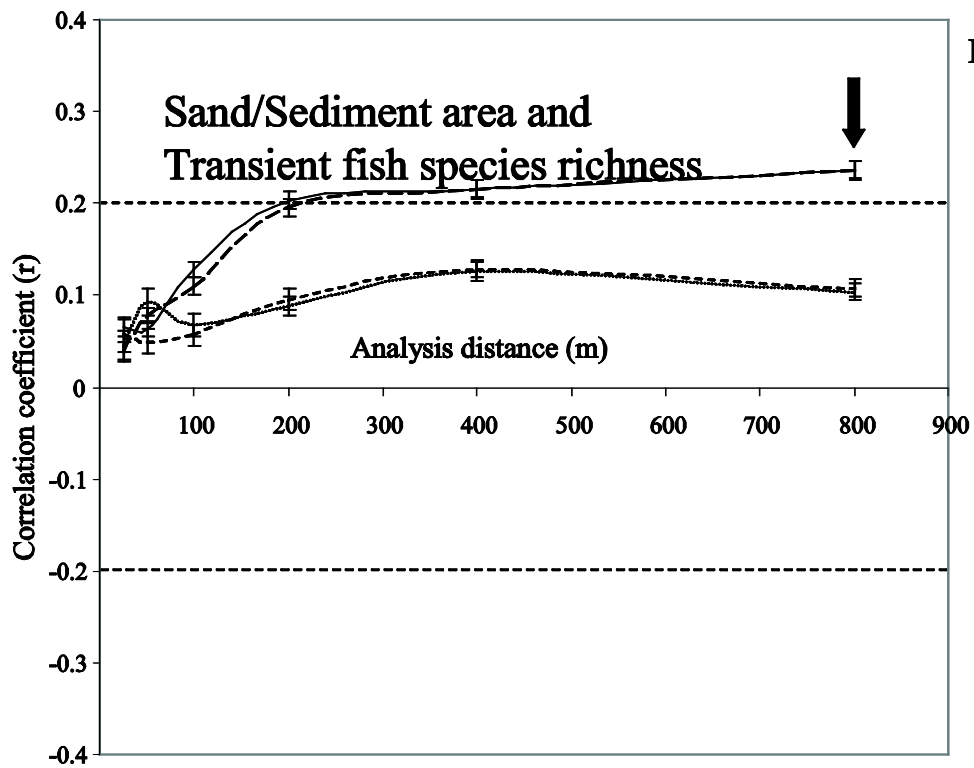
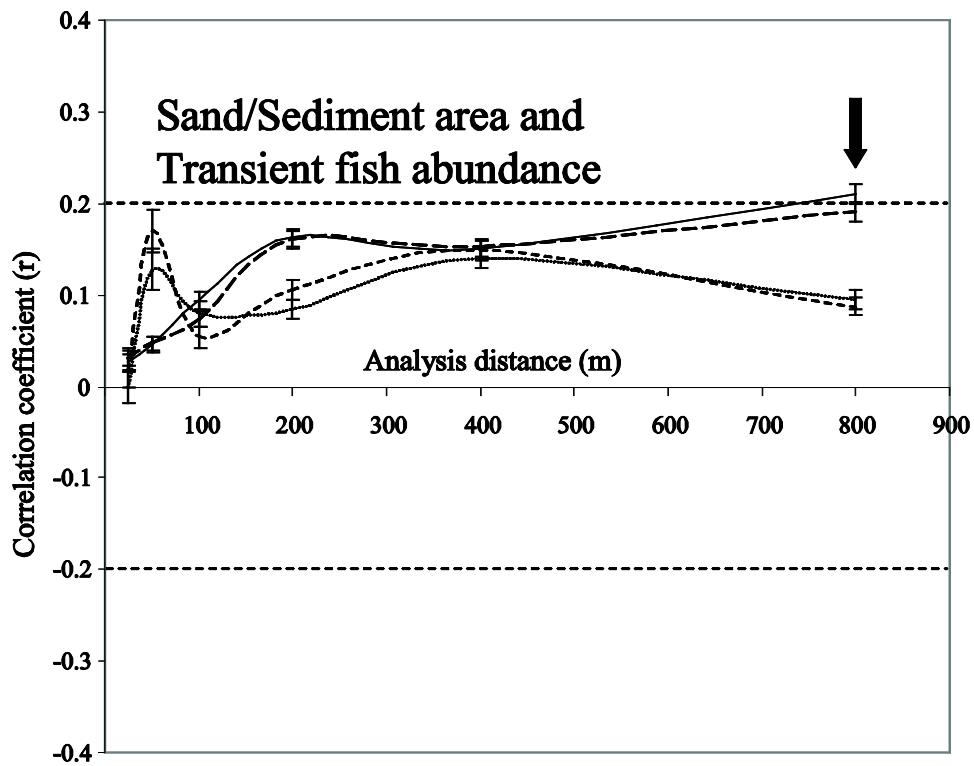


Figure 3b







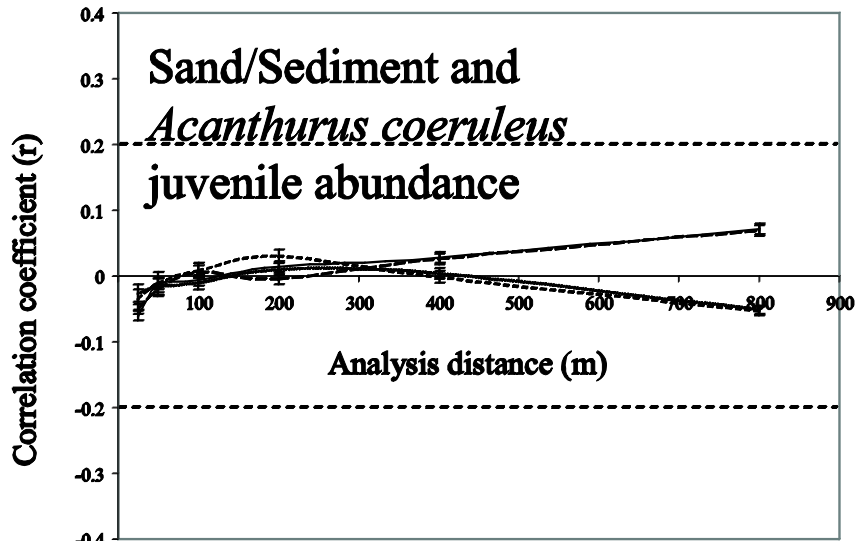


Figure 3i

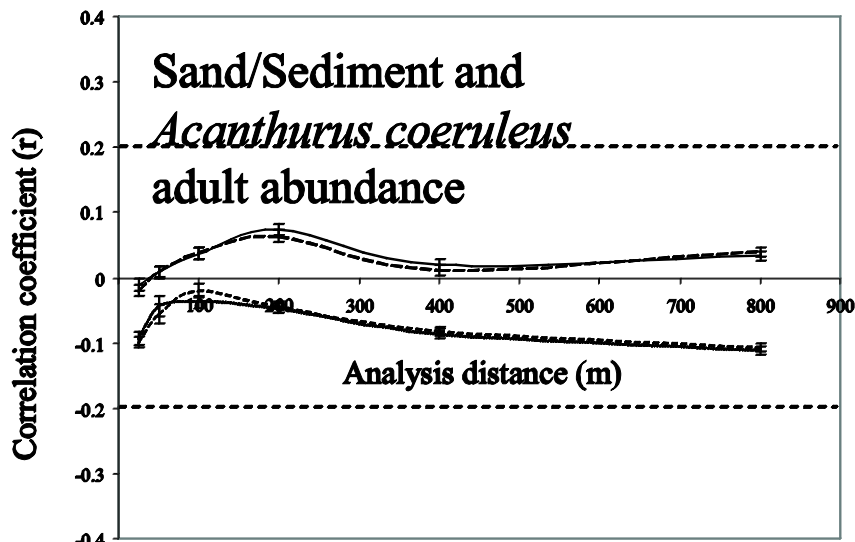


Figure 3j

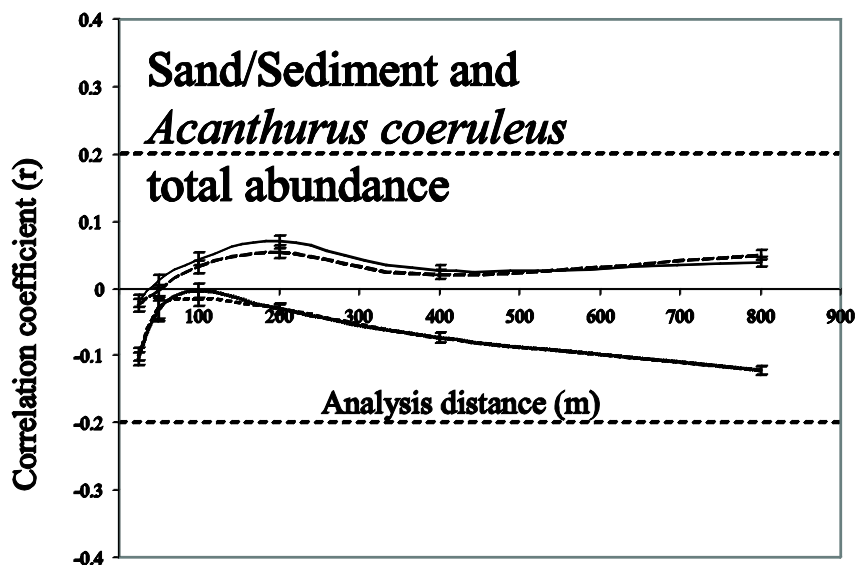


Figure 3k

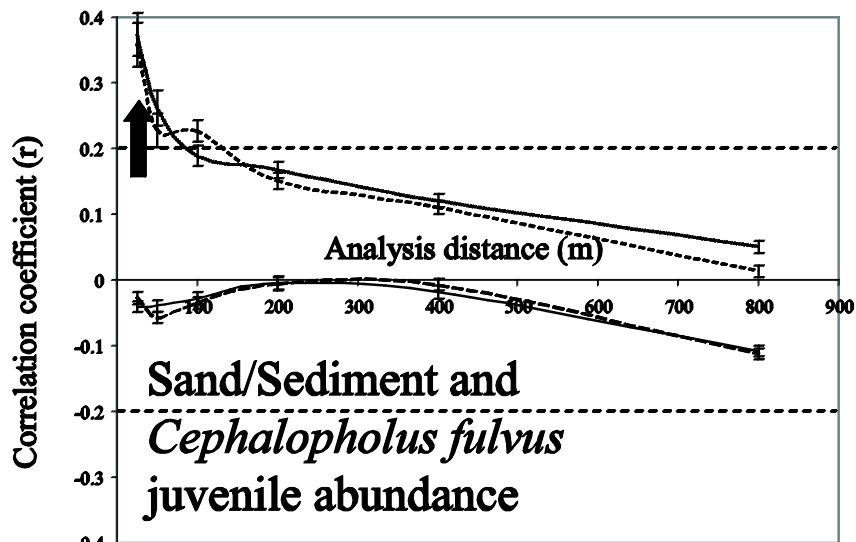


Figure 3l

ANOVA
 $p < 0.0001$

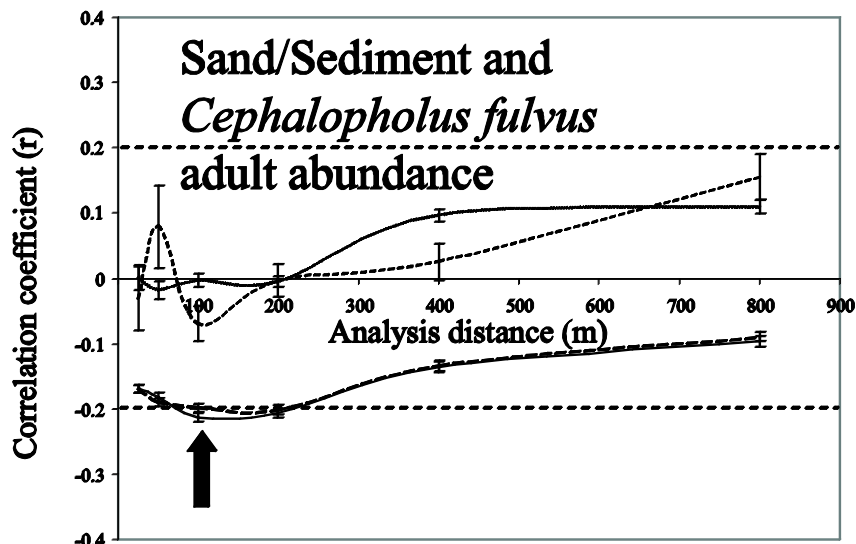


Figure 3m

ANOVA
 $p < 0.0001$

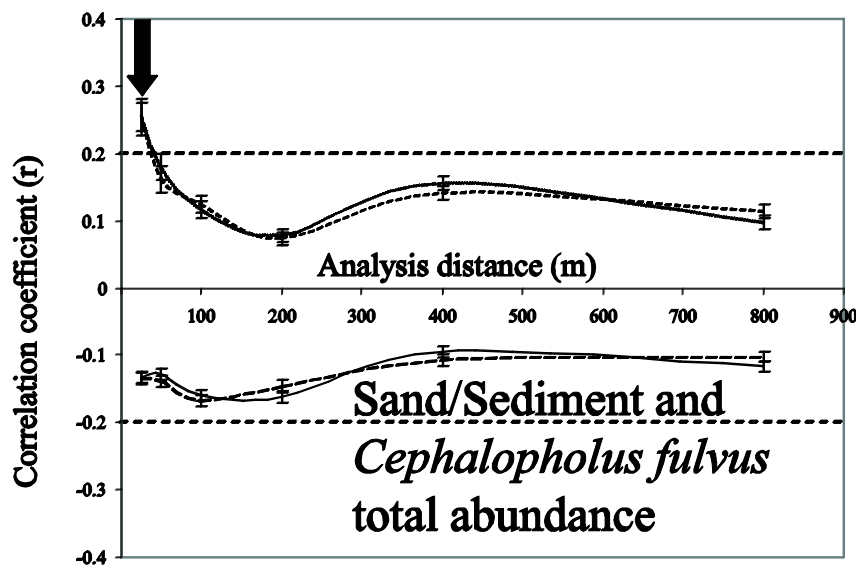


Figure 3n

ANOVA
 $p < 0.0001$

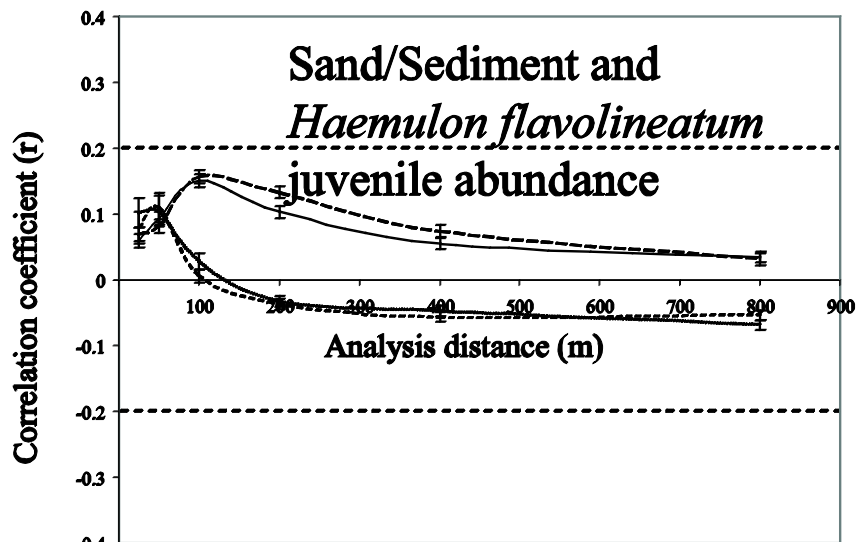


Figure 3o

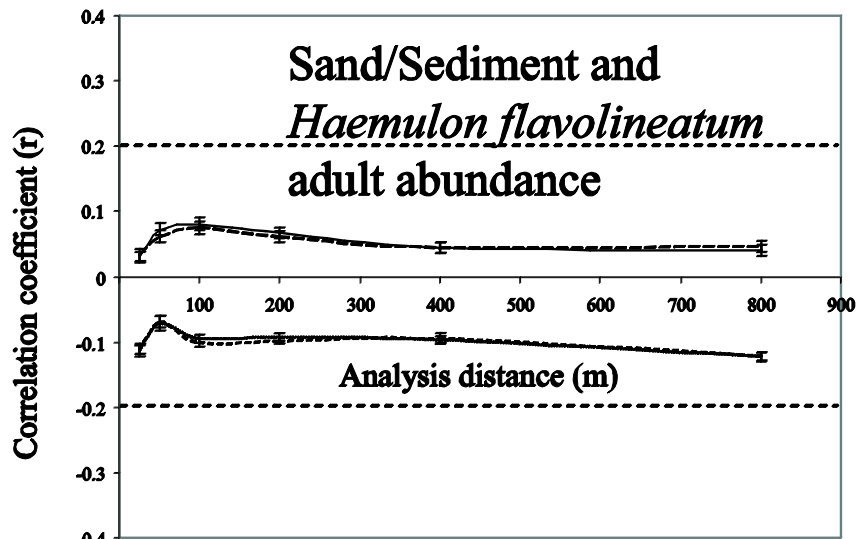


Figure 3p

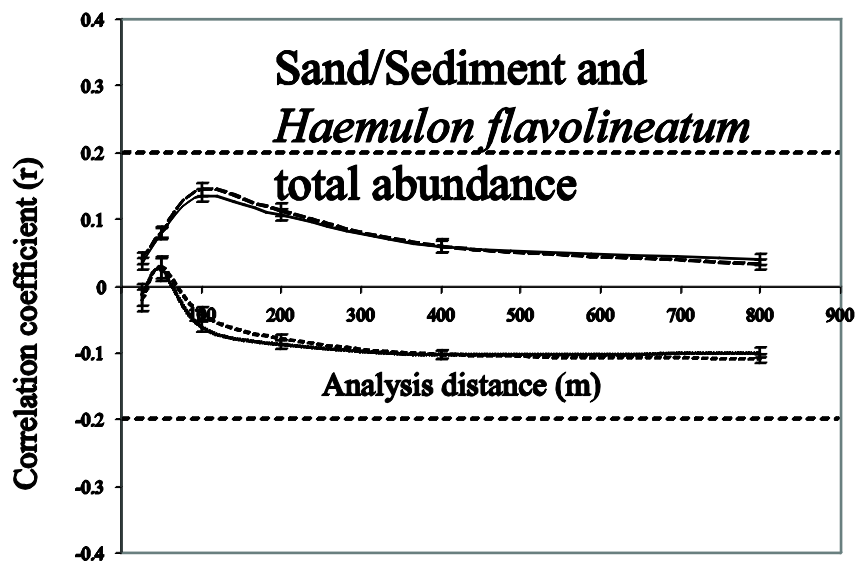
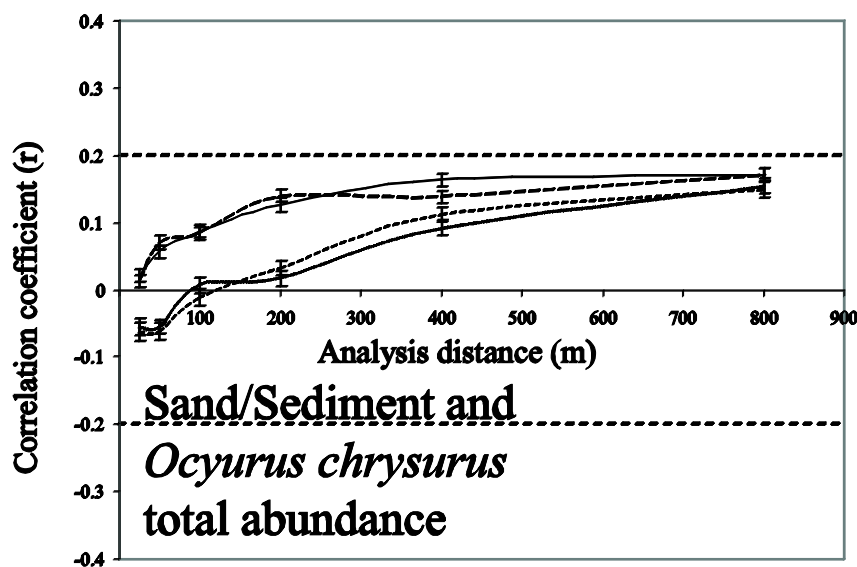
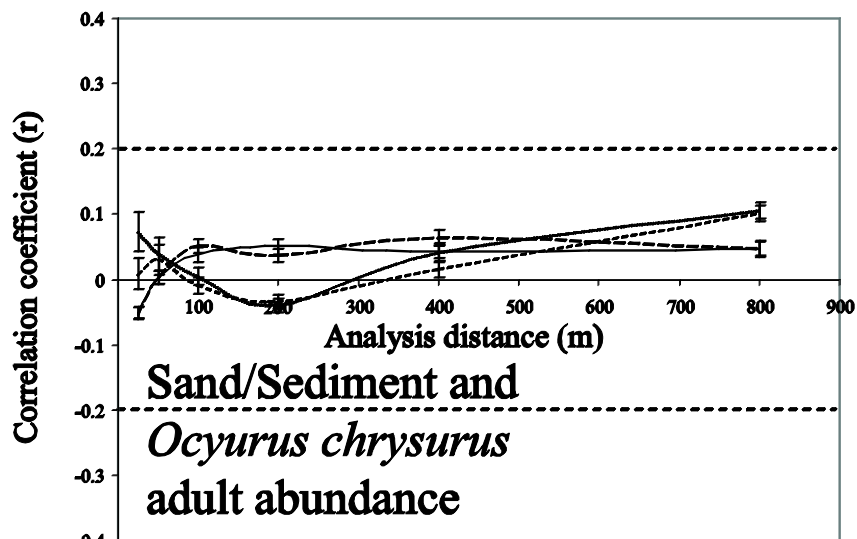
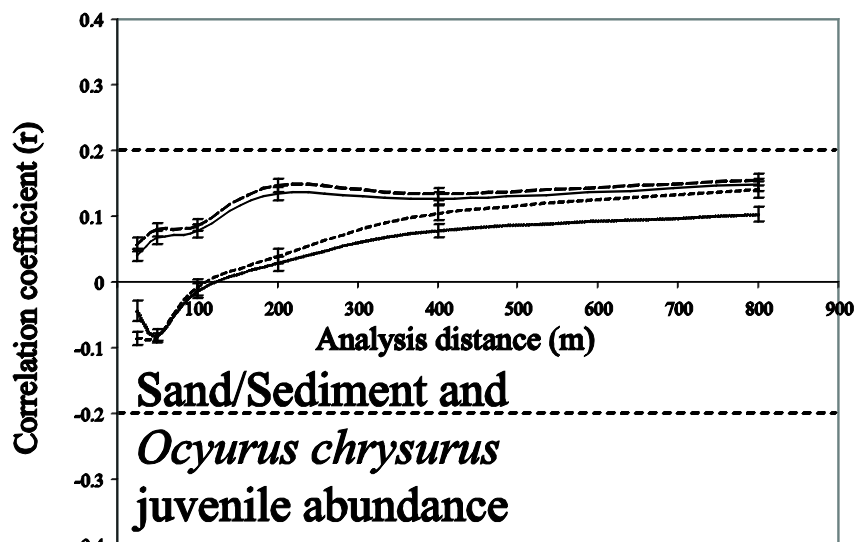


Figure 3q



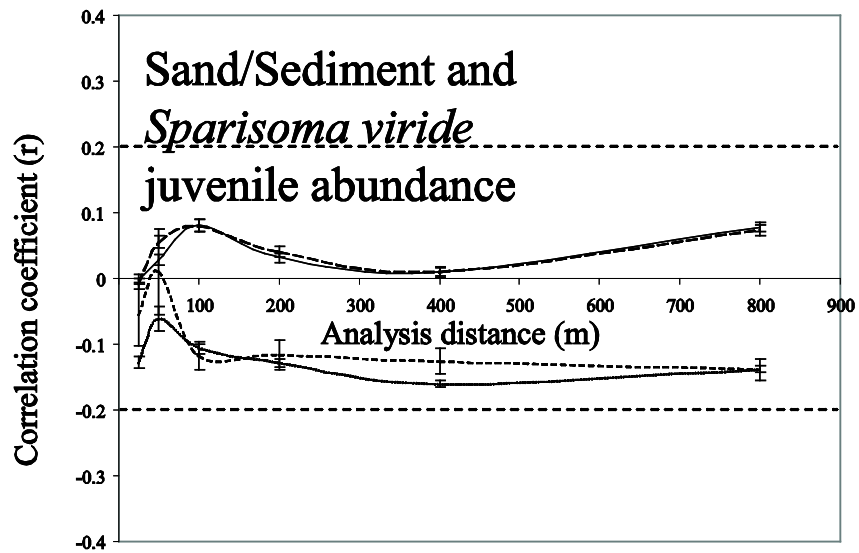


Figure 3u

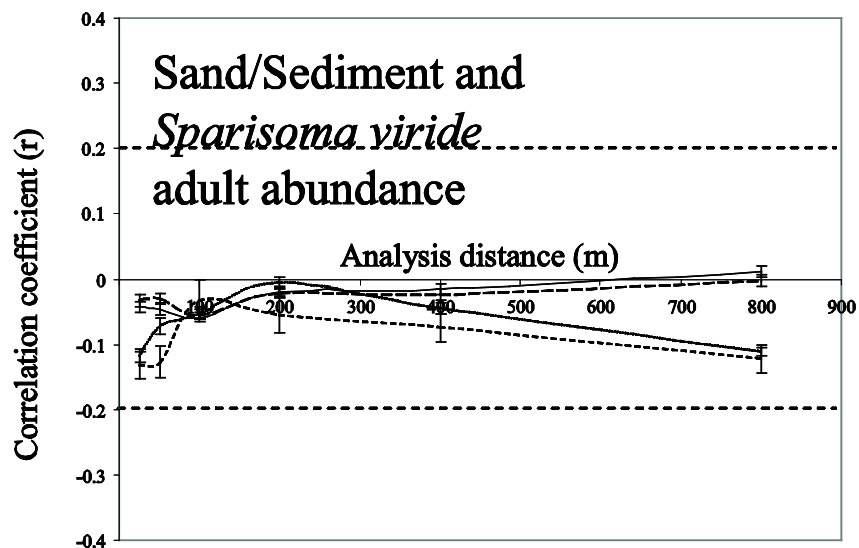


Figure 3v

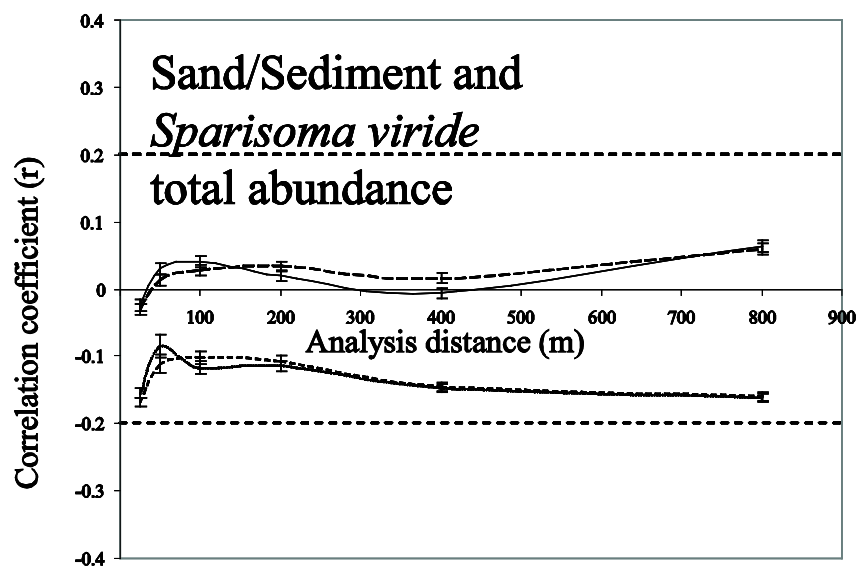


Figure 3w

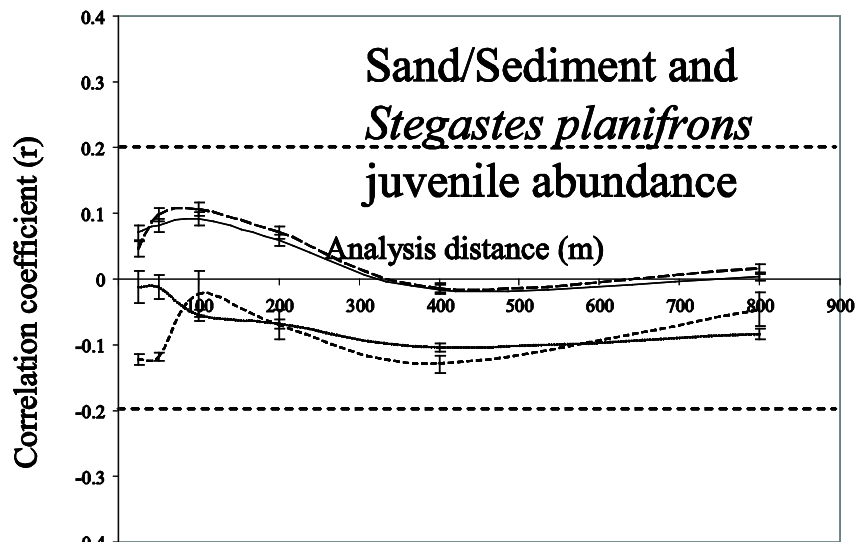


Figure 3x

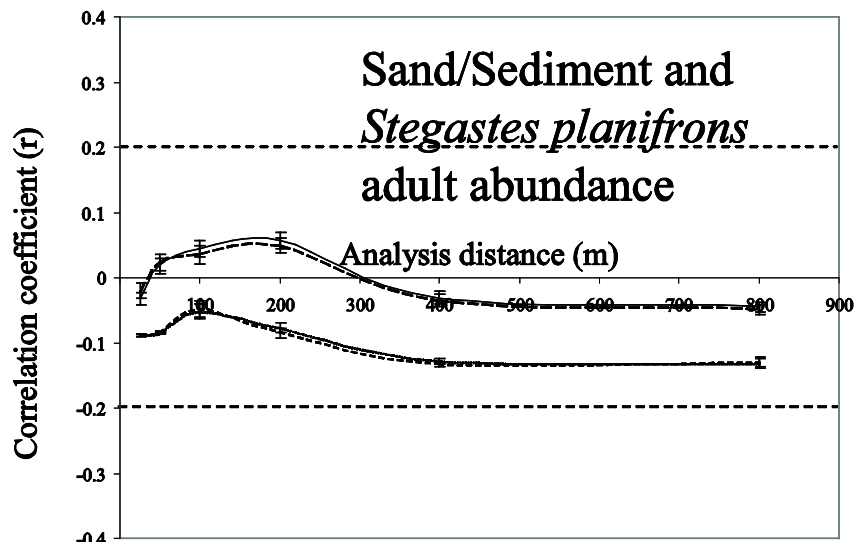


Figure 3y

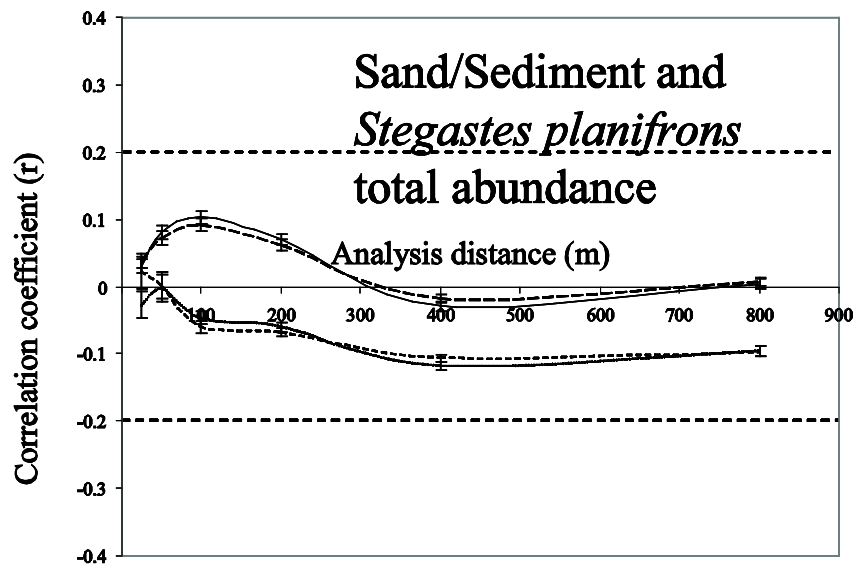


Figure 3z

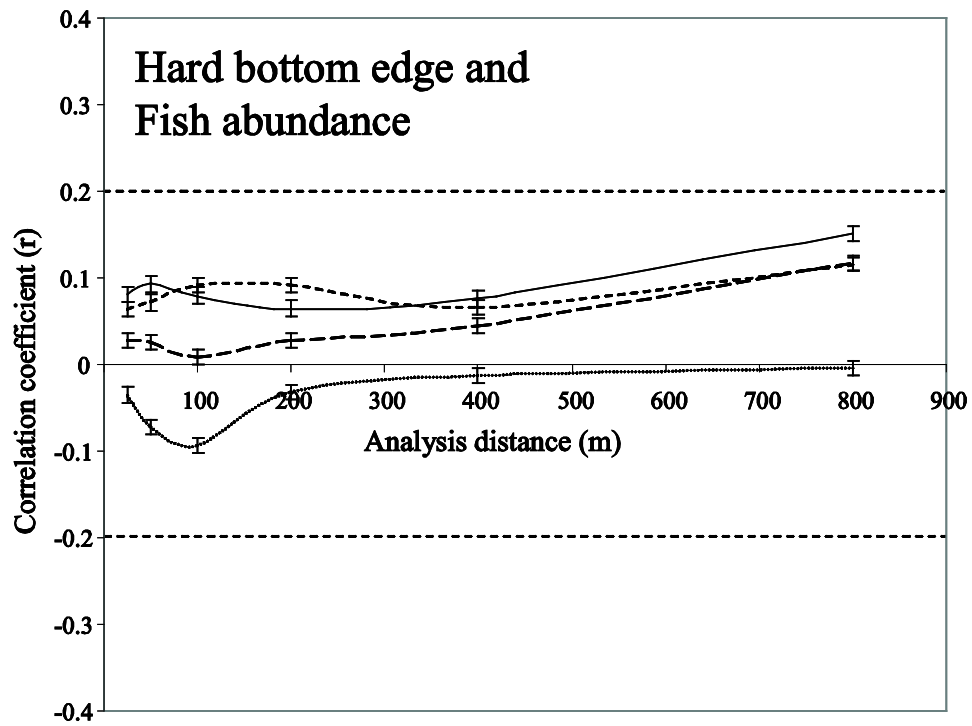


Figure 4a

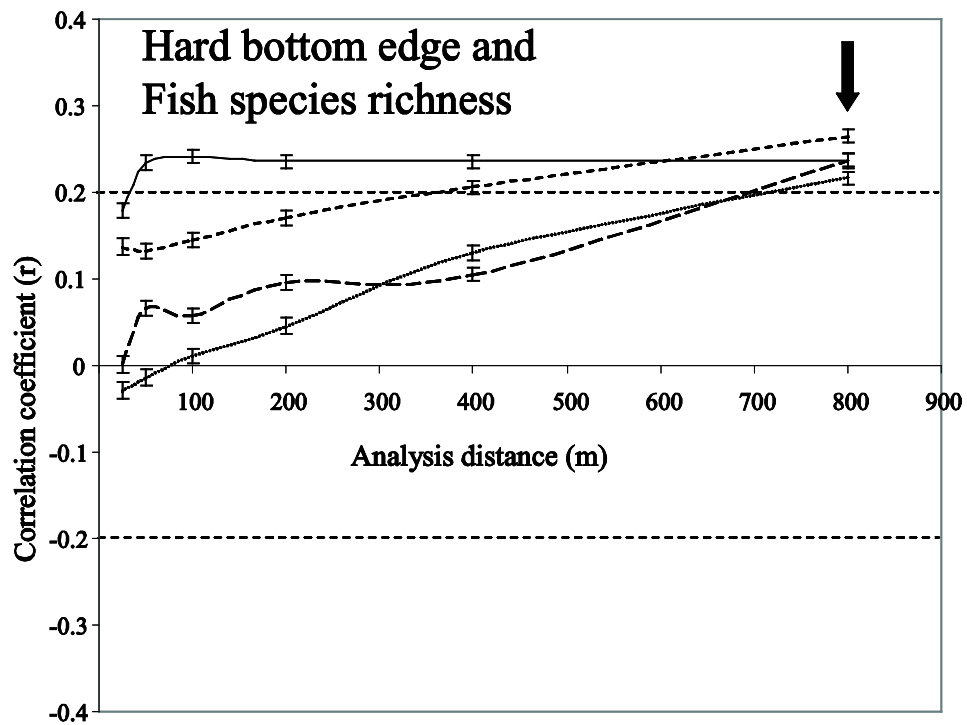
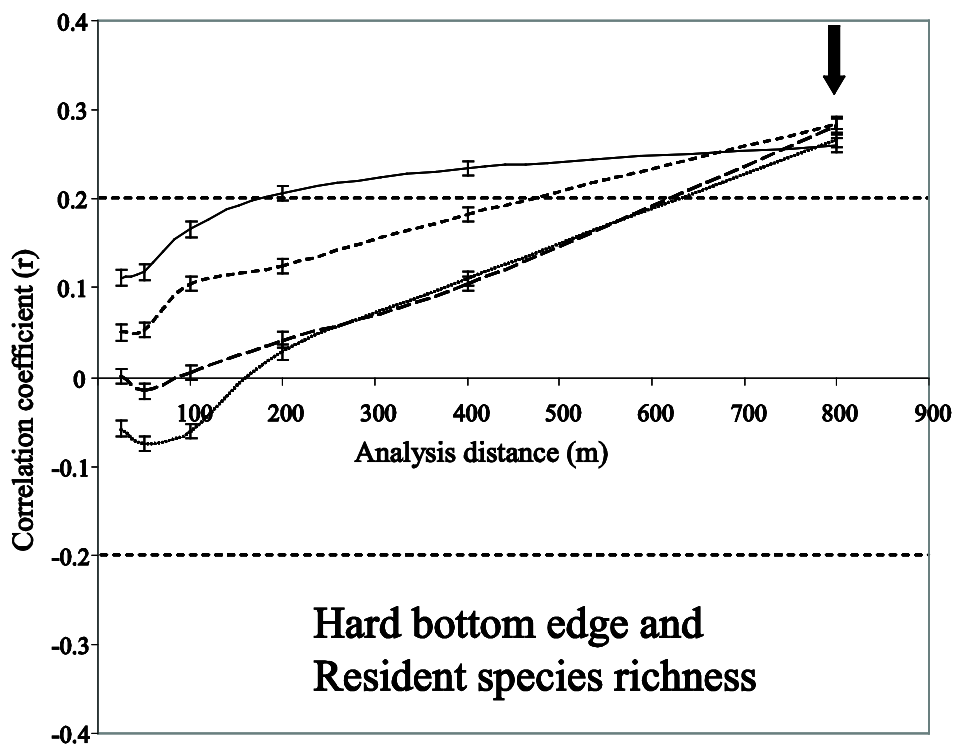
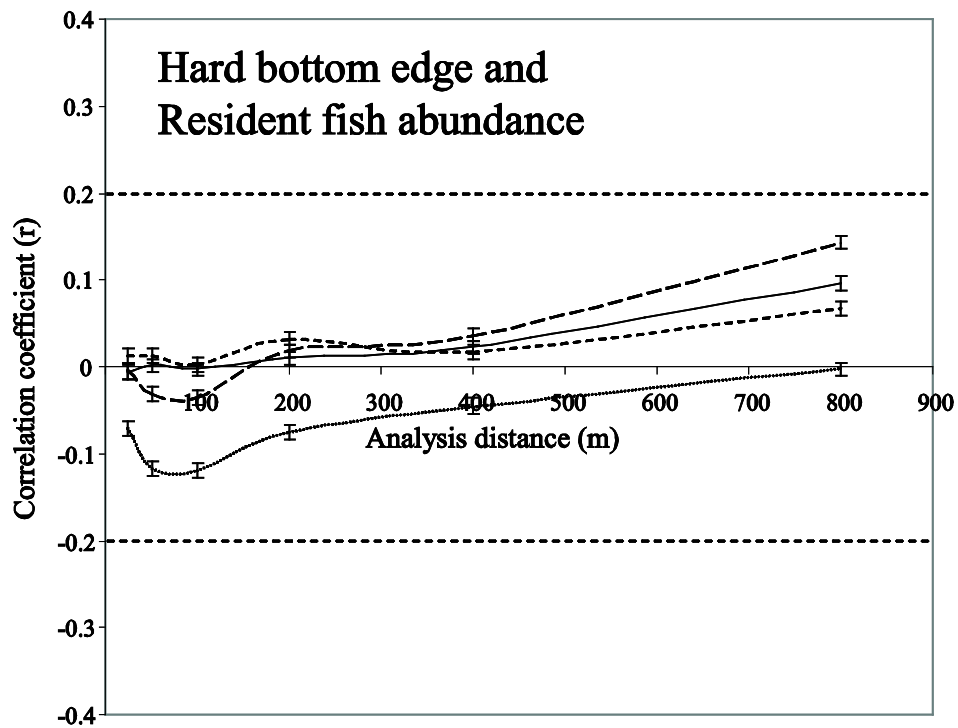
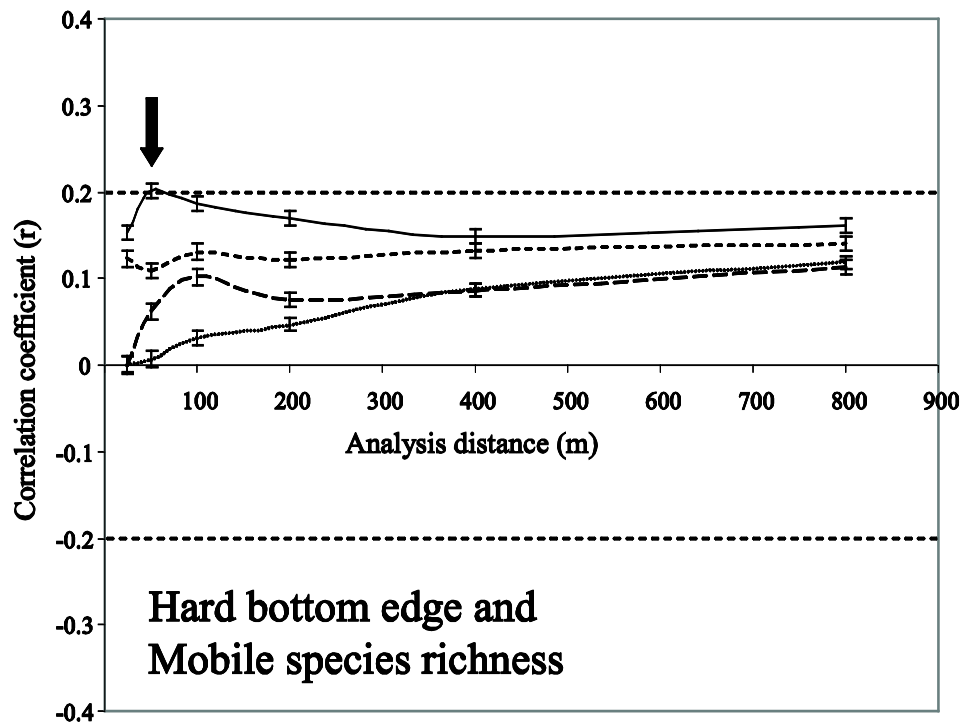
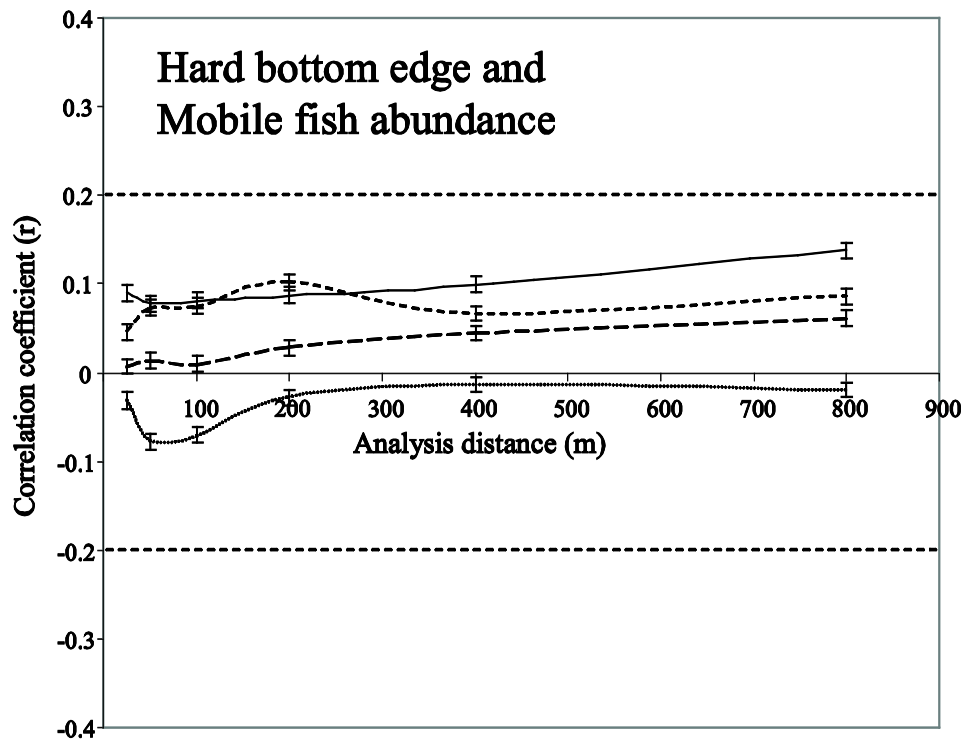
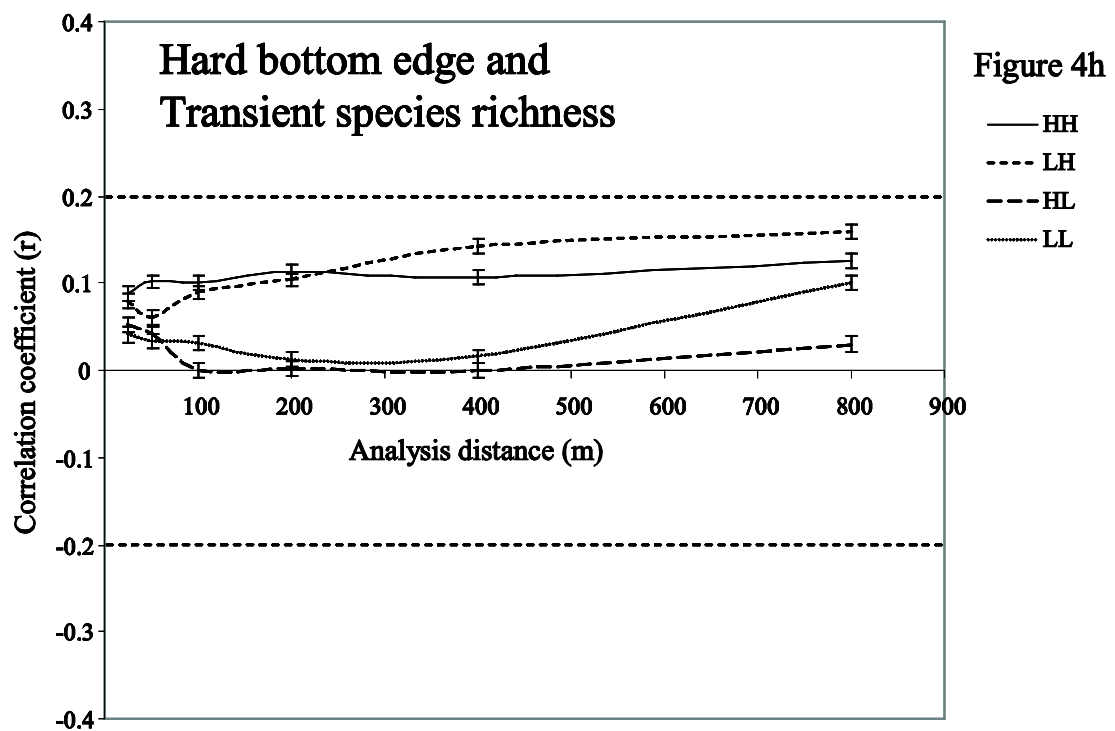
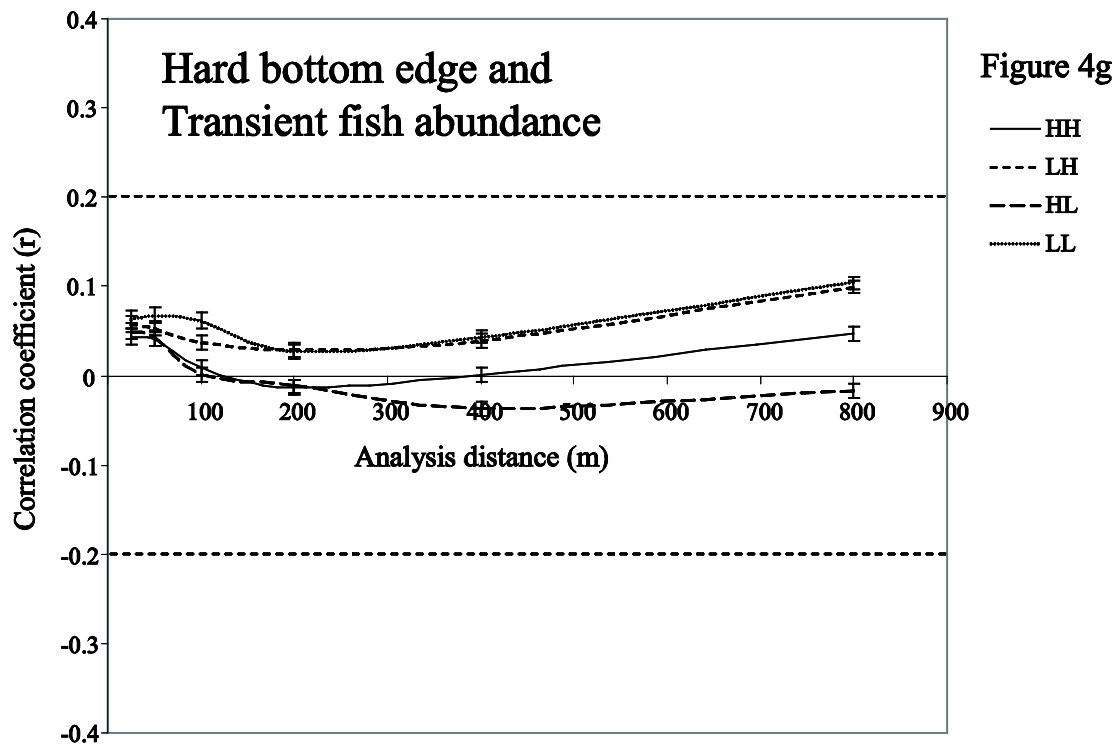
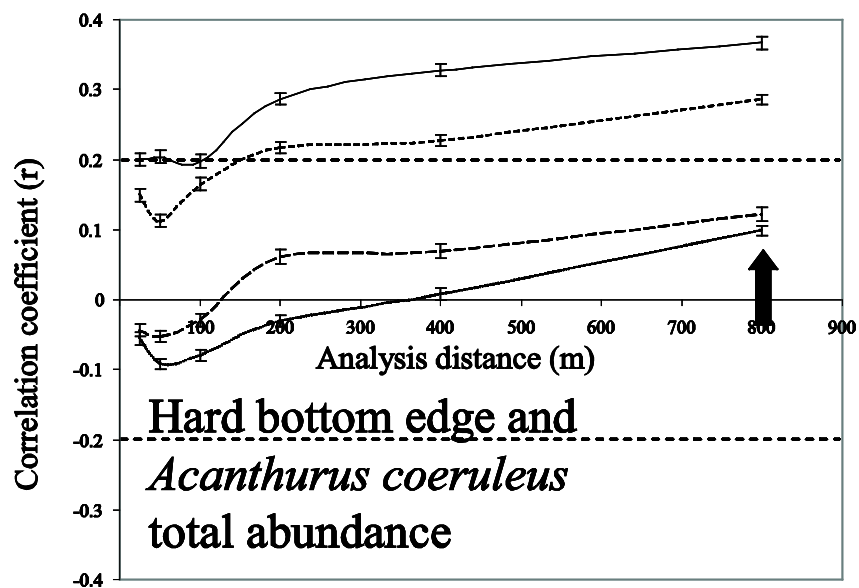
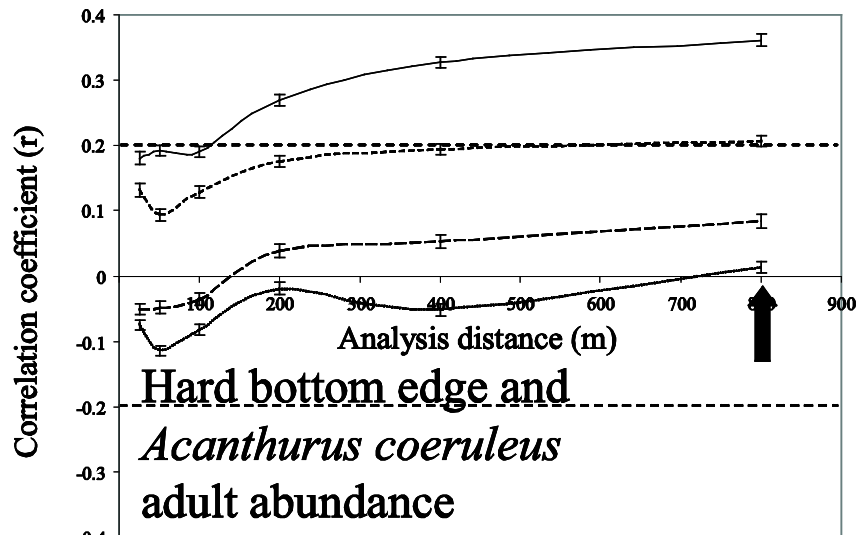
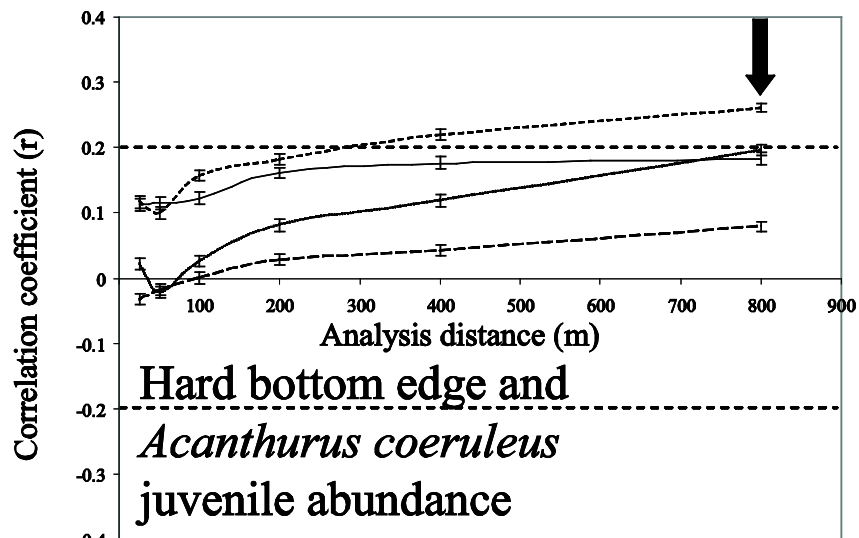


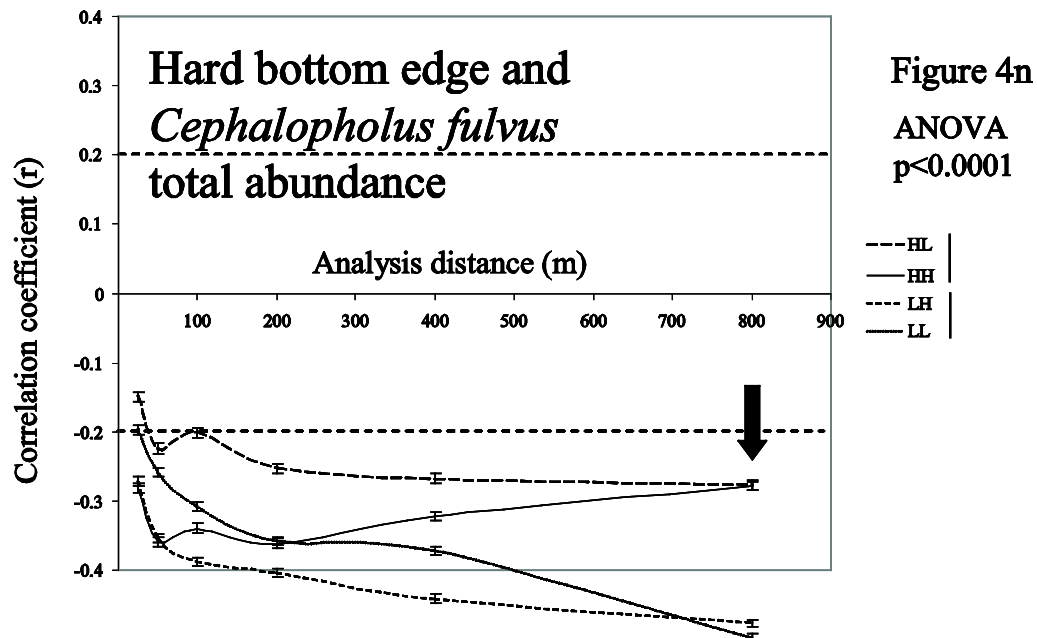
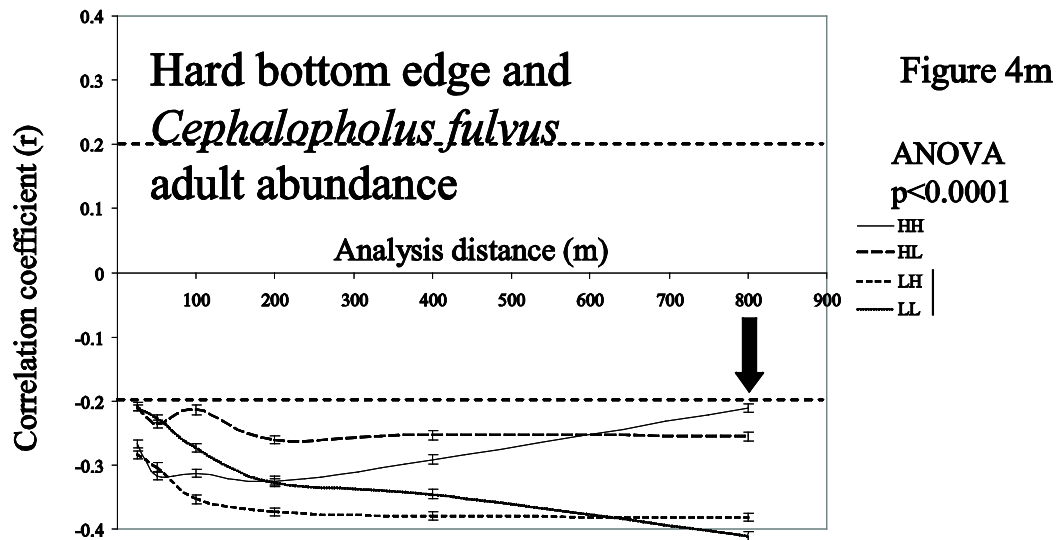
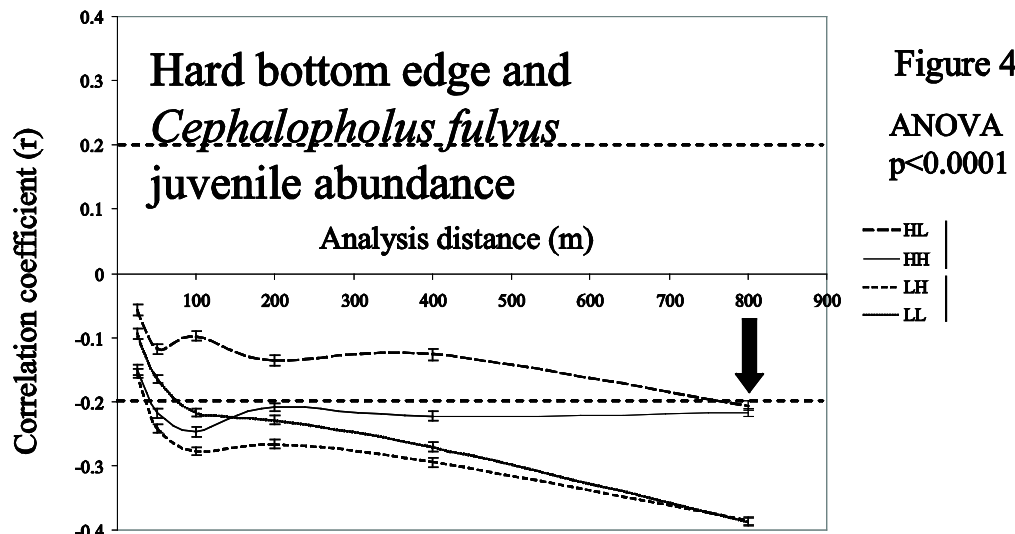
Figure 4b











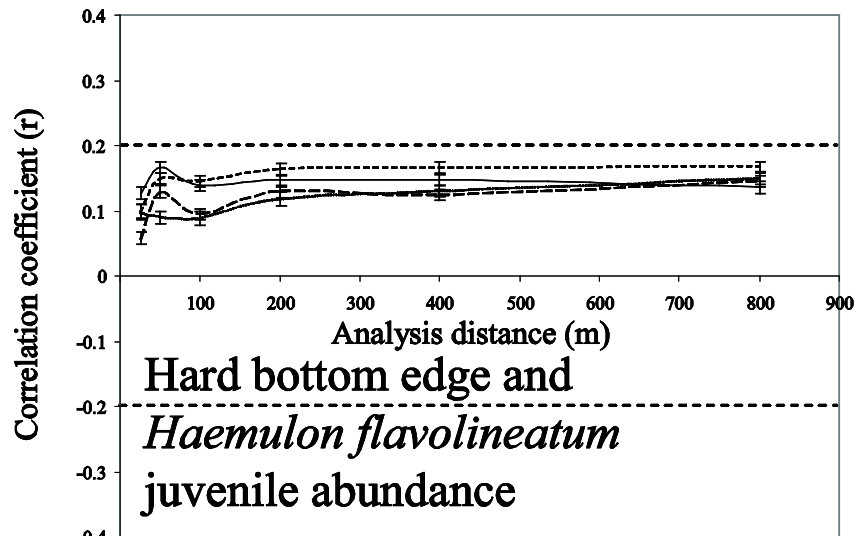


Figure 4o

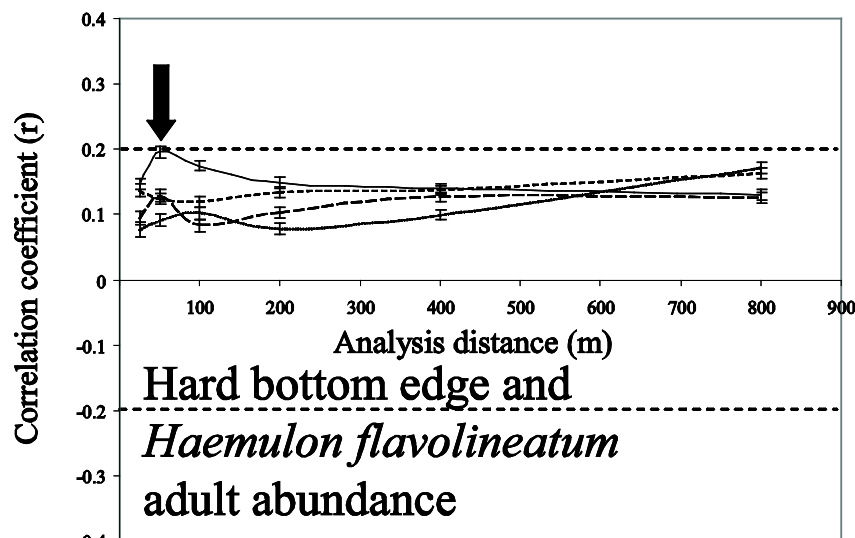


Figure 4p
ANOVA
 $p < 0.0001$

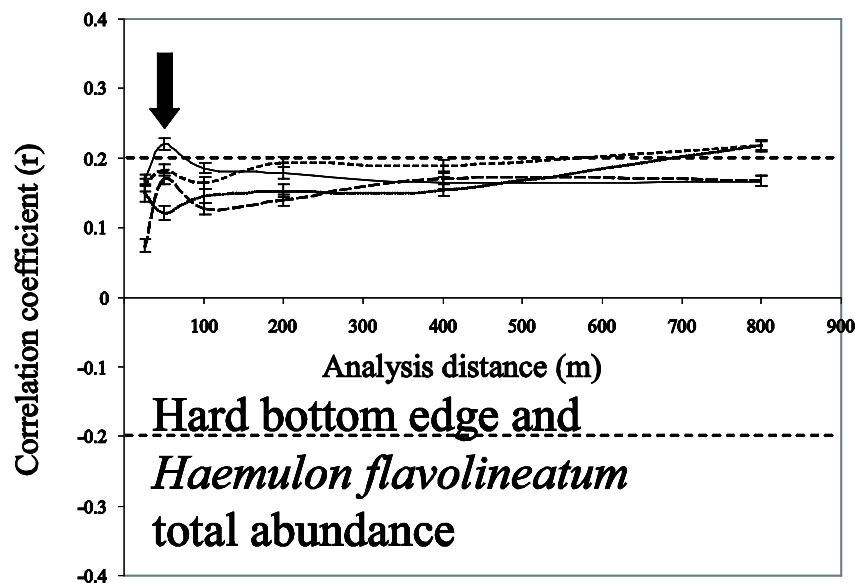


Figure 4q
ANOVA
 $p < 0.0001$

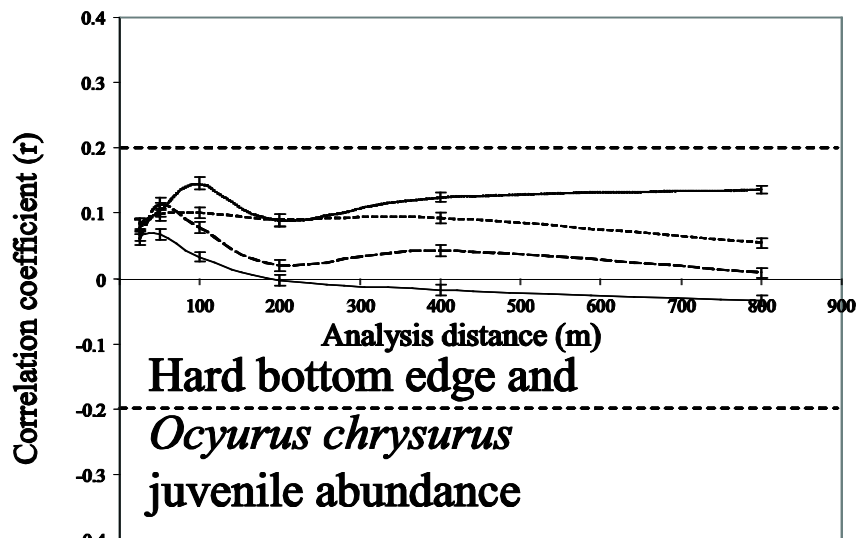


Figure 4r

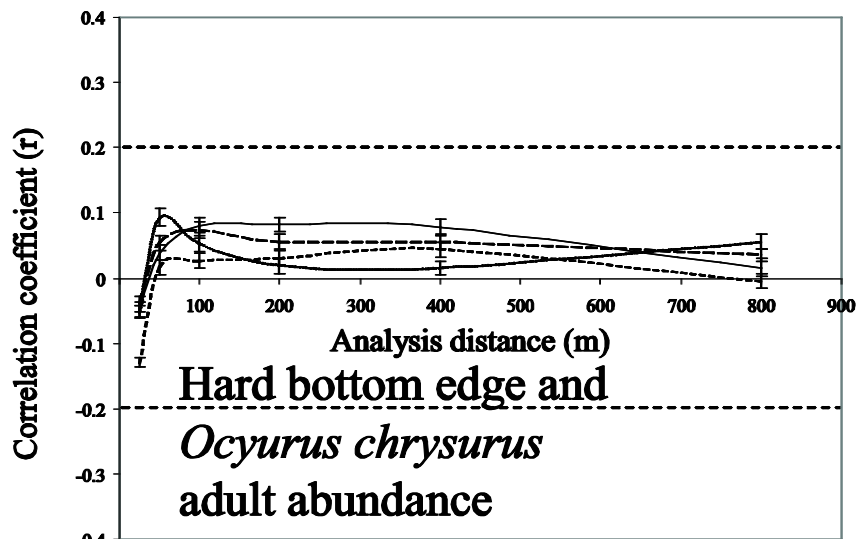


Figure 4s

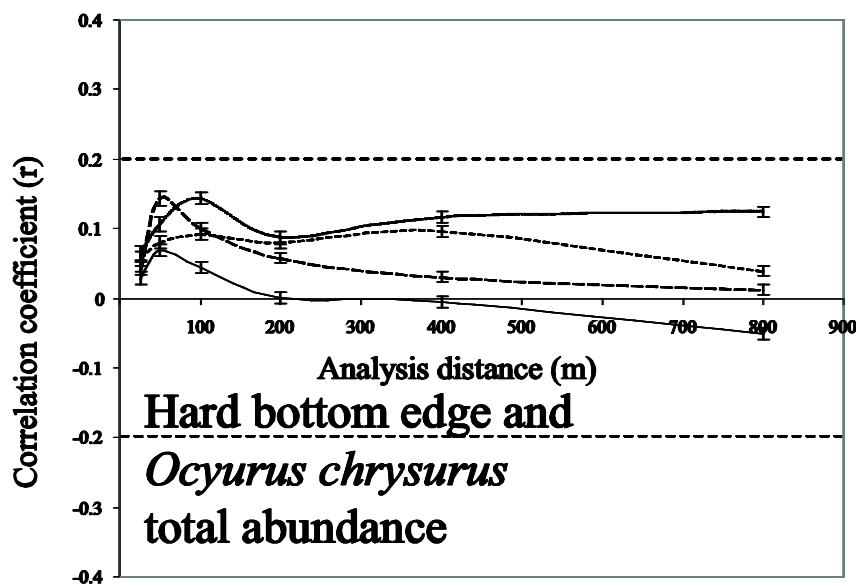


Figure 4t

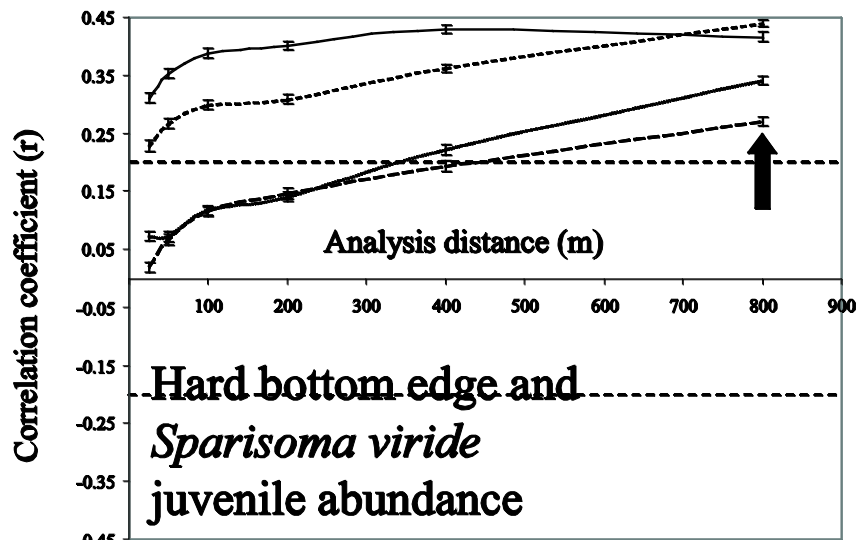


Figure 4u

ANOVA
p<0.0001

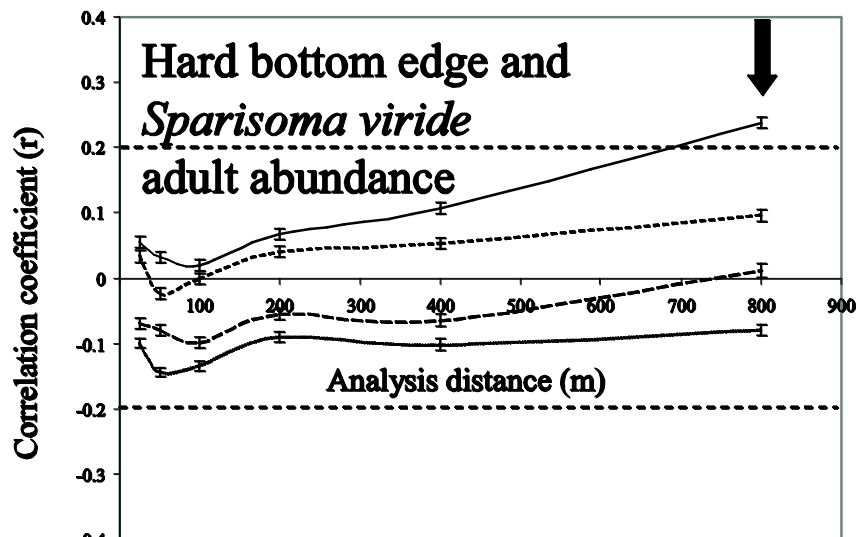


Figure 4v

ANOVA
p<0.0001

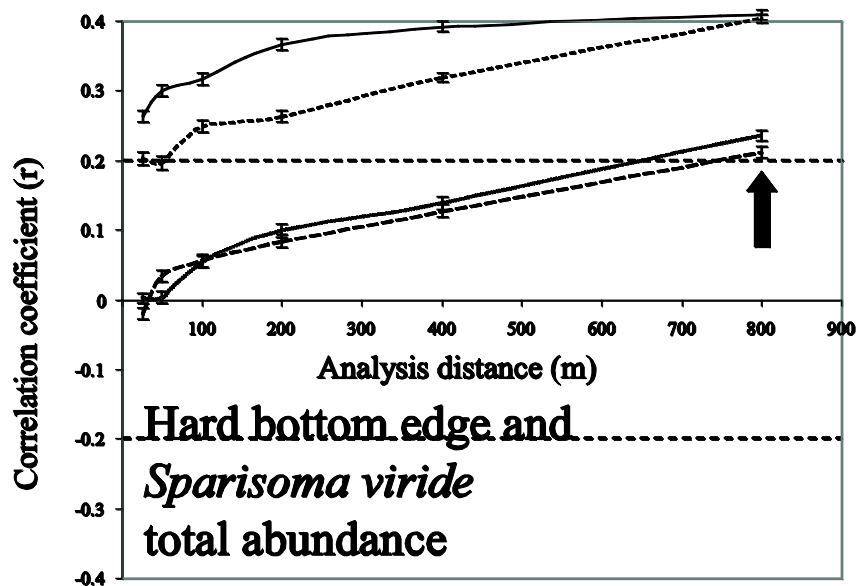


Figure 4w

ANOVA
p<0.0001

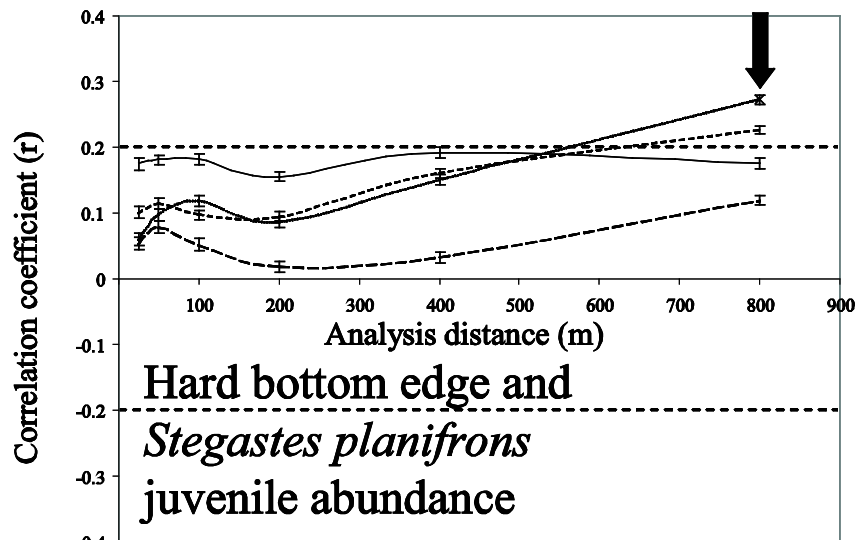


Figure 4x

ANOVA
 $p < 0.0001$

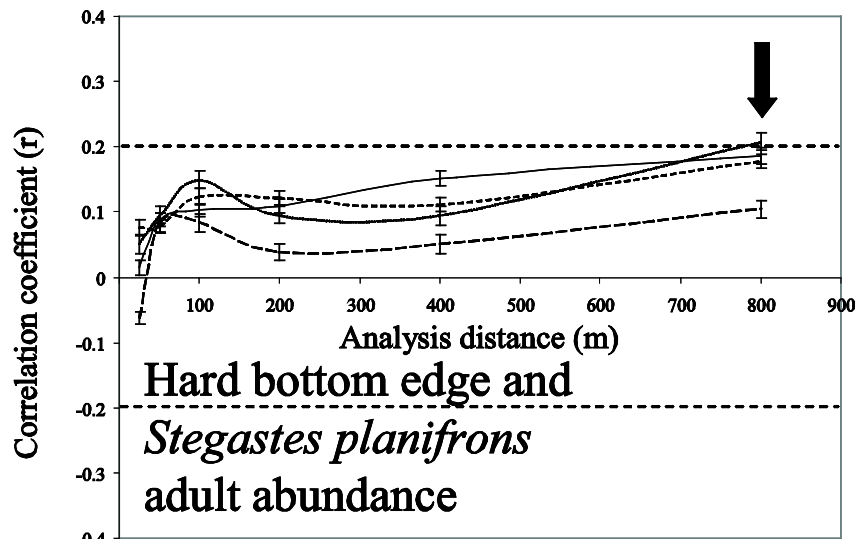


Figure 4y

ANOVA
 $p < 0.0001$

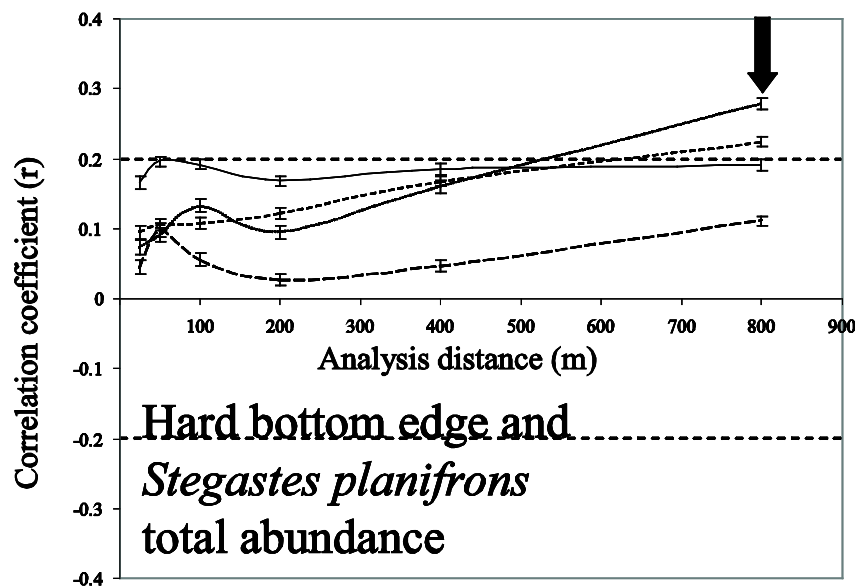


Figure 4z

ANOVA
 $p < 0.0001$

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